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SYNOPSIS OF BIOLOGICAL DATA ON GROUPERS

(*Epinephelus* and allied genera) OF THE WESTERN NORTH ATLANTIC

Prepared by

C. LAVETT SMITH

College of Guam, Agana, Guam

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Rome, December 1961

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SYNOPSIS OF BIOLOGICAL DATA ON GROUPERS (Epinephelus and allied genera) OF THE WESTERN NORTH ATLANTIC

Prepared by

C. Lavett Smith
College of Guam, Agana, Guam

FISHERIES DIVISION, BIOLOGY BRANCH
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Rome, December 1961

FAO Fish. Bio. Synop. no. 23

PURPOSE OF THIS SERIES

This is one of a series of synopses of biological data concerning species of aquatic organisms of economic importance. The primary purpose of this series is to make existing information readily available to fishery scientists, according to a standard pattern, and by so doing also to draw attention to gaps in knowledge. It is hoped that synopses in this series will be useful to scientists initiating investigations of the species concerned or of related ones; as a means of exchange of knowledge among those already working on the species, and as the basis for comparative study of fisheries resources.

The synopses are the output of a system for cumulative storage and retrieval of data on the biology of species and stocks, called Species and Stocks Thesaurus (SAST), maintained by the Fisheries Biology Branch of FAO. They will be brought up to date from time to time, as further information becomes available. It is, therefore, recommended that they be filed in loose-leaf folders; pagination begins anew with each chapter, so that partial revisions may be made.

Biology Branch is working to secure the cooperation of scientists in drafting synopses on species about which they have special knowledge, and welcomes offers of help in this task. Additions and corrections to synopses already issued will also be most welcome. Comments and requests for information should be addressed to the editor of this series:

Horacio Rosa, Jr.
Fisheries Division, Biology Branch
FAO of the United Nations
Viale delle Terme di Caracalla
Rome, Italy

PREPARATION OF THIS SYNOPSIS

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Fisheries workers concerned with this species

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1 IDENTITY

1.1 Taxonomy

1.1.1 Definition

Groupers may be defined as large serranid fishes of the genus Epinephelus and the allied genera Mycteroperca, Dermatolepis, Cephalopholis, Petrometopon, Alphestes, and Paranthias. This complex of genera has had a varied nomenclatoral history - some authors have accorded them full family rank, whereas others have considered them as two genera. As the relationships of many of the species now placed in the family Serranidae are poorly known, it seems best to withhold the assignment of any particular rank to the group and to indicate their mutual affinities by the common name "grouper".

The genera and species of groupers are closely related and are frequently not distinguished by commercial or sport fishermen. In fact, the United States Fish and Wildlife Service report entitled "Fishery Statistics of the United States 1957" lists only three categories, viz., Warsaw (Epinephelus nigritus /Holbrook/), Jewfish (Epinephelus itajara /Lichtenstein/), and grouper, this last term presumably including all other species. Much of the confusion in the names of groupers is due to the ability of individual groupers to assume various color patterns but, once these color phases are understood, groupers are no more difficult to identify than any other comparable group of fishes.

1.1.2 Description

The seven genera of Western Atlantic groupers share the following characters:

Moderate-sized to large serranid fishes with small ctenoid or secondarily cycloid scales numbering 60 to 140 in lateral series. Scales are present over the entire head and body except the lips, snout, and sometimes the exposed surfaces of the maxillae. Dorsal spines 9 to 11, dorsal soft rays 14 to 20. Anal spines 3, anal soft rays 8 to 13. Pectoral rays 16 to 20. Gill rakers 10 to 54 (total of both limbs of the first arch). Branchiostegal rays 7. Mouth large and terminal, usually with a supramaxillary bone. Strong caniniform or villiform teeth are present on the premaxillae, dentaries, vomer and palatines as well as the pharyngeal bones and usually the gill rakers. Lateral line single, continuous, well below the dorsal profile, and emerging through small intercalated scales on the body. Cephalic lateral line canals much branched with numerous pores. Dorsal fin single, usually with a shallow notch. Caudal fin rounded or slightly forked in all species except Paranthias furcifer (Valenciennes) in which it is deeply forked. Pectorals usually rounded. Pelvic fins bound to the body by membrane for about half the length of the last ray. There is a fleshy flap in the axil of the pectoral fin but no pelvic axillary process. The premaxillae are slightly protractile. There are strong supraoccipital and fronto-

parietal crests on the skull and these provide characters of generic importance.

Characters of the genera and species found in the Western North Atlantic are given in the following key.

KEY TO THE GENERA AND SPECIES OF THE GROUPERS OF THE WESTERN NORTH ATLANTIC

A. Caudal fin deeply forked; head short, less than 30 per cent of the standard length. Supramaxillary bone vestigial or absent..... ..... Paranthias furcifer (Val.).

A'. Caudal fin never deeply forked, usually rounded or lunate, sometimes with extended upper and lower lobes in large individuals. Head long, more than 33 per cent of standard length. Supramaxillary bone well developed.

B. Anal rays 8 to 10, usually 8 or 9.

C. Preopercle without a strong antrorse spine at its angle.

D. Dorsal spines usually 11 (sometimes 10 in Epinephelus nigritus).

E. Scales ctenoid, body only moderately compressed, usually reddish, brown or green; if black there are no distinct white spots. Pectoral fin less than 30 per cent of standard length..... .....Epinephelus.

F. Dorsal spines long, at least some as long as or longer than the anterior dorsal soft rays.

G. Body variously colored, if red spots are present these are not largest ventrally, and the maxillary is scaled on its exposed surface. Never more than one saddle-shaped dark blotch.

H. Posterior nostril never 3 or 4 times as large as the anterior. Color uniform, spotted, or with 5 to 7 irregular vertical bars.

I. Dorsal fin membrane not indented between the spines... ..... Epinephelus morio (Val.)

I'. Dorsal fin membrane indented between the spines.

J. Body with spots or bars or, if nearly uniform then there is a broad yellow margin on the spinous dorsal fin.

K. Body with 5 vertical bars, the 3rd and 4th branch and their branches fuse. A squarish dark saddle-shaped mark on the caudal peduncle. Several distinct dark spots below and behind the eye.....Epinephelus striatus (Bloch).

K'. Body without vertical bars, saddle-shaped marks present or absent. No spots around eye.

L. Body with red spots on a light background, no saddle-shaped mark on caudal peduncle.....Epinephelus guttatus (Linn.).

L'. Body usually with white spots in definite rows. If these spots are lost there is a wide yellow margin on the spinous dorsal fin. Saddle-shaped mark present.

M. Margin of spinous dorsal dusky. Saddle-shaped mark on caudal peduncle reaches below the lateral line. No light line on cheek.....Epinephelus niveatus (Val.).

M'. Margin of the spinous dorsal and anterior part of the soft dorsal yellow. Saddle-shaped mark not reaching below lateral line. A narrow, pale line from eye to angle of preopercle.....Epinephelus flavolimbatus (Poey).

J'. Body nearly uniform in coloration, without definite markings.

N. Dorsal spine 10 or 11, elongate in the adult with the membrane deeply cleft between the spines. Body black or reddish brown above, lighter below, young with scattered white spots..... Epinephelus nigritus (Holbrook)

N'. Dorsal spines not especially elongate in the adult, always 11. Dorsal interspinous membrane not deeply cleft between the spines. Body reddish with indistinct white markings which sometimes tend to form vertical bars..... Epinephelus guaza (Linn.).

H'. Posterior nostril much enlarged, 3 or 4 times the diameter of the anterior. Color pattern consisting of 9 or 11 evenly spaced regular vertical bars. Sometimes two of these bars on the caudal peduncle unite to form a single broad dark band. This band is darkest dorsally, sometimes appearing as a saddle-shaped blotch.....
.....Epinephelus mystacinus (Poey)

G'. Body light with dark red spots which are much larger on the ventral surface. Three saddle-shaped blotches along the base of the dorsal fin and on top of the caudal peduncle. No scales on the exposed surface of the maxillary bone.....
.....Epinephelus adsconsionis (Osbeck) .

F'. Dorsal spines very short in specimens longer than 250 mm shorter than the shortest anterior soft rays. Color gray or greenish with small dark spots, very young specimens with oblique, irregular dark bands. Reaches a weight of 700 pounds.....
.....Epinephelus itajara (Lichtenstein)

E'. Scales smooth. Body rather strongly compressed, usually black with distinct white spots but sometimes gray with distinct black spots. Pectoral elongate, usually more than 30 per cent of the standard length.....
.....Dermatolepis inermis (Val.)

D'. Dorsal spines 9.

O. Body brownish, red, or yellow, with at least a few blue spots each about 2 mm in diameter and surrounded by a black ring. Two dark spots at tip of the lower jaw and two more on top of caudal peduncle. Pectoral rays normally 18....Cephalopholis fulva (Linn.)

O'. Body brownish or reddish with bright red spots each about 3 mm in diameter and not surrounded by a black ring. No dark spots at tip of lower jaw or on top of caudal peduncle but there are usually 3 or 4 small distinct spots along the base of the dorsal fin. Pectoral rays usually 16.....
.....Petrometopon cruentatum (Lacépède)

C'. Preopercle with a strong antrorse spine at its angle..... .....Alphestes afer (Bloch)

B'. Anal soft rays usually 10 to 13..... Mycteroperca

P. Gill rakers 7 to 18 on lower limb of first arch.

Q Preopercle rounded, without a distinct spiny lobe or abrupt angle.

R. Vertical fins of large adults (those over 50 cm) without exserted soft rays. Color pattern never consisting of 11 oblique light lines on a darker background.

S. Pectoral fin with a broad yellow distal margin, sharply delimited from the spotted basal part. This yellow area includes the outer third of the fin. Color pattern on body consisting of irregular longitudinal rows of rounded dark blotches on a greenish or bright red background..... .....Mycteroperca venenosa (Linn.)

S'. Pectoral fin with a narrow orange margin grading into the darker basal part. This margin not over one-fifth of the fin length wide. Side of body with regular rows of rectangular dark blotches, or with a chain-like pattern of pale lines separating dark brownish spots..... .....Mycteroperca bonaci (Poey)

R'. Vertical fins of adults over 50 cm in length with exserted rays (i.e. some of the fin rays extending beyond the margin of the rest of the fin). Color pattern consisting of about 11 narrow light lines sloping downward and forward..... .....Mycteroperca tigris (Val.)

Q'. Preopercle with the upper and lower limbs meeting at nearly a right angle, with a more or less distinct serrated lobe at the angle above which is a slight notch.

T. Scales very small, about 120 to 140 in lateral series. Posterior nostril only slightly larger than the anterior in fish under 350 mm, somewhat larger in fish over this length. Vertical fins never with exserted rays. Color gray without distinctive markings or with dark vermiculations which tend to be grouped in squarish or rounded clusters ..... Mycteroperca microlepis (Goode and Bean)

T'. Scales larger, usually fewer than 120 in lateral series. Posterior nostril much larger than the anterior in individuals more than 250 mm long. Vertical fins of large specimens with exserted rays. Color brownish, uniform, or with a dense pattern of small dark spots.

U. Body light grayish brown, with distinct small spots arranged in clusters which are squarish or round ..... Mycteroperca phenax Jordan and Swain

U'. Body dark brown, uniform or with a reticulum of light lines separating small rounded or hexagonal spots which are not arranged in clusters..... Mycteroperca interstitialis (Poey)

P'. Gill rakers more than 30 on lower limb of first arch ..... Mycteroperca rubra (Bloch)

1.2 Nomenclature

1.2.1 Valid scientific names

1.2.2 Synonyms

Valid scientific names and short synonymies are given for each species that occurs in the Western North Atlantic on the following pages. An attempt has been made to include nearly all of the combinations as well as the generic and specific names that have been applied to these groupers.

Paranthias furcifer (Valenciennes)

Serranus furcifer Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, p.264, 1828 (Brazil)
Anthias furcifer Günther, Cat.Fishes British Mus., vol.1, p.91, 1859
Brachyrhinus furcifer Poey, Enumeratio, p.19, 1875 (Cuba)
Paranthias furcifer Guichenot, Ann.Soc.Linn. Maine-et-Loire, vol.10, p.87, 1868
Serranus creolus Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, p.265-6, 1828 (Port-au-Prince, Martinique, Santo Domingo)
Brachyrhinus creolus Gill, Proc.Acad.Nat.Sci.Phila., vol.14, p.249-50, 1862 (Lower California)
Paranthias creolus Guichenot, Ann.Soc.Linn. Maine-et-Loire, vol.10, p.87, 1868
Corvina oxyptera DeKay, New York Fauna; Fishes, pp.77-8, pl.30, fig.96, 1842
Epinephelus oxypterus Gill, Proc.Acad.Nat.Sci. Phila.Suppl.p.30, 1861
Serranus colonus Valenciennes, Voy.Vemus, p.300, pl.2, fig.1, 1855 (Galapagos Is)
Centropristis nebulosus Castelnau, Animaux Nouveaux ou Rares de l'Amerique du Sud, p.5, pl.1, fig.4, 1855 (Brazil)
Serranus castelnaui Jordan and Eigenmann, Bull.U.S.Fish.Comm., vol.8 (1888), p.409, 1890 (substitute name)
Paranthias pinguis Walford, Occ.Paps.Santa Barbara Mus.Nat.Hist.no.4, pp.2-3, 1936 (Guaymas, Mexico)

Epinephelus striatus (Bloch) (Fig.1, p.1:24)

Cherna Parra, Dif.Piezas Nat.Hist.Cuba, p.50, pl.24, fig.1, 1787 (Cuba)
Anthias cherna Bloch and Schneider, Syst.Ichth., p.310, 1801
Anthias striatus Bloch, Nat.Ausl.Fische, vol.6, pp.125-6, pl.324, 1792 (Atlantic Ocean, on a figure by Plumier)
Serranus striatus Valenciennes, in Cuvier and Valenciennes, Hist.Nat. Poiss., vol.2, pp.288-91, 1828
Epinephelus striatus Poey, Repertorio, vol.2, p.285, 1868 (Cuba)
Cerna striata Miranda Ribeiro, Fauna Brasiliense, Peixes V., p.16, 1915 (Brazil)
Sparus chrysomelanus Lacépède, Hist.Nat.Poiss., vol.4, p.160, 1802 (Martinique)
Serranus gymnopareius Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, pp.248-9, 1828

Epinephelus morio (Valenciennes)

Serranus morio Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, pp.285-6, 1828 (New York, Santo Domingo)
Epinephelus morio Gill, Proc.Acad.Nat.Sci.Phila., Suppl.vol.13, p.30, 1861
Cerna morio Miranda Ribeiro, Fauna Brasiliense, Peixes V, pp.18-9, 1915 (Brazil)
Serranus erythrogaster DeKay, New York Fauna; Fishes, pp.21-3, pl.19, fig.52 1842
Epinephelus eyrthrogaster Gill, Proc.Acad.Nat.Sci.Suppl.vol.13, p.30, 1861
Serranus remotus Poey, Memorias, vol.2, pp.140-1, 1860 (Cuba)
Serranus angustifrons Steindachner, Verh.Ges.Wien, vol.14, p.230, pl.7, figs.2-3, 1864 (Cuba)
? Epinephelus angustifrons Jordan, Proc.U.S.Nat.Mus.vol.9, p.580, 1887 (after Steindachner)
Dermatolepis angustifrons Jordan and Eigenmann, Bull.U.S.Fish.Comm., vol.8 (1888), pp.375-6, 1890
? Cherna americana Jordan, Bull.U.S.Fish Comm., vol.4, p.78, 1884 (Florida Keys)
Epinephelus guativere (not of Parra) Garman, Bull.Lab.Nat.Hist.State Univ.of Iowa, vol.4, pp.77-8, 1896 (Tortugas)

Epinephelus guttatus (Linnaeus) (Fig.1, p.1:24)

Perca guttata Linnaeus, Syst.Nat., ed.10, p.292, 1758 (America, after Catesby)
Epinephelus guttatus Goode, Bull.U.S.Nat.Mus.5, p.58, 1876 (Bermuda)
Serranus guttatus Fowler, Proc.Acad.Nat.Sci.Phila., vol.80, p.470, 1928 (St. Lucia)
Cabrilla Parra, Dif.Piezas Nat.Hist.Cuba, p.93, pl.36, fig.1, 1787
Lutianus lumulatus (not of Park) Bloch, in Bloch and Schneider, Syst.Ichth., p.329, 1801 (after Parra)
Serranus lunulatus Valenciennes, In Cuvier and Valenciennes, Hist.Nat. Poiss., vol.2, pp.379-80, 1828 (after Bloch)
Epinephelus lunulatus Poey, Repertorio vol.2, p.286, 1868
Serranus maculosus Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, pp.332-3, 1828
Epinephelus maculosus Jordan and Evermann, Rept.U.S.Comm.Fish and Fish., vol.21, (1894-1895), p.372, 1896
? Serranus nigriculus Valenciennes, in Cuvier and Valenciennes, Hist.Nat. Poiss., vol.2, pp.375-6, 1828 (Martinique)

Serranus arara (not of Parra) Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, pp.377-8, 1828 (Martinique)
Serranus catus Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss,, vol.2, pp.373-5, 1828 (Martinique)
Epinephelus catus Jordan Proc.U.S.Nat.Mus., vol.9, p.40, 1886
Cerna catus Miranda Ribeiro, Fauna Brasiliense, Peixes V., pp.16-7, 1915 (Brazil)
Serranus maculatus Günther, Cat.Fishes British Mus., vol.1, p.130, 1859
Serranus pixanga (not of Valenciennes) Poey, Repertorio, vol.1, p.203, 1866
Serranus apua (not of Bloch) Steindachner, Ichth, Notizen, VI, p.43, 1867 (Barbados)
Epinephelus apua Jordan and Swain, Proc.U.S.Nat.Mus.vol.7, pp.389-91, 1884
Epinephelus cubanus Poey, Repertorio, vol.1, p.202, 1866 (Cuba)
Epinephelus sp.dub. Poey, Repertorio, vol.2, p.287, 1868 (Cienfuegos, Cuba)
Serranus Stathouderi Vaillant and Bocourt, Miss.Sci.Mexico. Poiss., p.69, 1877 (substitute for maculosus, preoccupied)

Epinephelus drummondhayi (Goode and Bean)

Epinephelus drummond-hayi Goode and Bean, Proc.U.S.Nat.Mus., vol.1, pp.173-5, 1878 (Bermuda and Florida)
Serranus drummond-hayi Fowler, Proc.Acad.Nat.Sci.Phila., vol.80, p.453, 1929 (Tortugas)

Epinephelus niveatus (Valenciennes) (Fig.1, p.1:24)

Serranus niveatus Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, p.380, 1828 (Brazil)
Epinephelus niveatus Poey, Repertorio, vol.2, p.286, 1868
Garrupa niveata (part) Miranda Ribeiro, Fauna Brasiliense, Peixes, V, pp.19-20 (Brazil)
Serranus conspersus (part) Poey, Memorias, vol.2, pp.139-40, 1860
Serranus margaritifer Günther, Cat.Fishes British Mus.vol.1, pp.131-2, pl.9, fig.B, 1859 (South America)
Hyporthodus flavicauda Gill, Proc.Acad.Nat.Sci.Phila., vol.13, pp.98-9, 1862 (Newport, Rhode Island)
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Epinephelus mystacinus (not of Poey) Longley and Hildebrand, Carnegie Inst. Wash.Publ.535, pp.94-5, 1941 (Tortugas)

Epinephelus flavolimbatus Poey (Fig.2, p.1:25)

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Serranus flavolimbatus Fowler, Proc.Acad.Nat.Sci.Phila.,vol.59, p.252 1907 (San Domingo)
Epinephelus niveatus (not of Poey) Jordan and Evermann, Proc.U.S.Nat.Mus. vol.9, p.475, 1887 (Gulf of Mexico)
Serranus conspersus (part) Poey,Memorias, vol.2, pp.139-40, 1860

Epinephelus nigritus (Holbrook) (Fig.2, p.1:25)

Serranus nigritus Holbrook, Ichth.South Carolina, ed.1, p.173, pl.25, fig.2 1855 (Charleston, reference not seen)
Epinephelus nigritus Gill, Proc.Acad.Nat.Sci.Phila.Suppl.vol.13, p.30, 1861
Garrupa nigrita Jordan and Evermann, Rept.U.S.Fish Comm., vol.21 (1894-5), p.373, 1896
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Alphestes scholanderi Walters, Copeia no.4, pp.283-6, 1957 (Bimini)

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Serranus mystacinus Poey, Memorias, vol.1, pp.52-3, pl.10, fig.2, 1851 (Cuba)
Epinephelus mystacinus Jordan and Swain, Proc.U.S.Nat.Mus.vol.7, pp.383-4 (Havana)
Schistorus mystacinus Poey, Repertorio, vol.2, pp.154-5, 277, 1868
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Perca adscensionis Bonnaterre, Tableau Encyclo., p.132, 1788
Epinephelus ascensionis Jordan, Bull.U.S.Fish.Comm., vol.4, p.78, 1884 (Key West)
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Serranus ascensionis Fowler, Bull.Amer.Mus.Nat.Hist., vol.70, pp.757-9 fig.334, 1936 (Eastern Atlantic)

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Perca maculata Bloch, Nat.Ausl.Fische, vol.6, p.92-3, pl.313, 1792 (Atlantic and Antilles)
Serranus maculatus Peters, Akad.Wissen.Berlin, (1865), p.109, 1866
Trachinus osbeck Lacépède, Hist. Nat.Poiss., vol.2, p.364, 1800
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Epinephelus aspersus Jordan and Eigenmann, Bull.U.S.Fish Comm., vol.8 (1888), p.358, 1890 (after Jenyns)
Serranus nigriculus Valenciennes, in Cuvier and Valenciennes, Hist.Nat. Poiss., vol.2, p.375, 1828
Serranus impetiginosus Müller and Troschel, in Schomburgk, Hist.Barbados, p.665, 1848 (Barbados)
Epinephelus impetiginosus Jordan and Gilbert, Bull.U.S.Nat.Mus.16, p.573, 1883
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Epinephelus capreolus Jordan and Gilbert, Bull.U.S.Nat.Mus.16, pp. 539-40, 1883
Serranus varius Bocourt, Ann.Sci.Nat., vol.10, p.222, 1868 (Gulf of Mexico)
Epinephelus punctatus Fowler, Fish Cult., vol.21, p.68, 1942 (Cuba)
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Epinephelus analogus (not of Gill) Borodin, Bull.Vanderbilt Oceanogr.Mus., vol.1, no.4, p.112, 1934

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Serranus itajara Lichtenstein, Abhandl.Berlin Akad.Wiss. (1821), pp.278-9, 1822 (Brazil)
Promicrops itajara Schultz, Proc.U.S.Nat.Mus., vol.99, p.121, 1949 (Venezuela)
Serranus itaiara Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, pp.376-7, 1828 (amended spelling)
Promicrops itaiara Jordan and Swain, Proc.U.S.Nat.Mus., vol.7, pp.377-9 1884
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Serranus galeus Müller and Troschel, in Schomburgk, Reise British Guiana, p.621, 1848
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Serranus guaza (not of Linnaeus) Poey, Memorias, vol.2, pp.141-2, tab.13, fig.8, 1861 (Cuba)
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Epinephelus quinquefasciatus Jordan and Gilbert, Bull.U.S.Fish Comm., vol.2, p.106, 1883 (Mazatlan)
Promicrops guttatus (not of Linnaeus) Jordan and Eigenmann, Bull.U.S.Fish. Comm., vol.8 (1888), pp.363-4, pl.62, 1890 (Brazil)
Epinephelus nigritus (not of Holbrook) Henshall, Bull.U.S.Fish. Comm., vol.9 (1889), p.387, 1891 (Florida)

Epinephelus guaza (Linnaeus) (Fig.3, p.1:26)

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Serranus guaza Fowler, Proc.Acad.Nat.Sci.Phila., vol.59, p.253, 1907 (Italy, Syria)
Epinephelus guaza Jordan and Eigenmann, Rept.U.S.Comm.Fish, vol.21 (1894-95), p.372, 1896
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Serranus gigas Valenciennes, in Cuvier and Valenciennes, Hist.Nat. Poiss., vol.2, p.270-8, 1828
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Serranus guaza mentzelii Fowler, Proc.Acad.Nat.Sci.Phila., vol.59, pp.253-4, 1907
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Serranus dichropterus Valenciennes, in Cuvier and Valenciennes, Hist.Nat. Poiss., vol.2, pp.293-4, 1828 (Brazil)
Perca robusta Couch, Mag.Nat.Hist., vol.5, p.21, fig.7, 1832 (Cornwall)
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Serranus fimbriatus Lowe, Trans. Cambridge Philos.Soc., pp.195-6, tab.1, figs.1-2, 1838 (Madeira)
Serranus ongus (not of Bloch) Günther, Cat.Fishes, British Mus., vol.1, pp.142-3, 1859 (Brazil)
Epinephelus brachysoma Cope, Trans.Amer.Philos.Soc., vol.14, p.466, 1871 (Rio de Janeiro)

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Serranus inermis Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.9, pp.436-7, 1833 (Antilles)
Lioperca inermis Poey, Repertorio, vol.2, p.282, 1868
Dermatolepis inermis Jordan and Swain, Proc.U.S.Nat.Mus., vol.7, pp.405-6, 1884 (Havana)
Epinephelus inermis Boulenger, Cat.Fishes. British Mus., ed.2, vol.1, p.257, 1895 (West Indies)
Dermatolepis zanclus Evermann and Kendall, Bull.U.S.Fish.Comm., vol.17, (1897), pp.129-30, pl.8, fig.9, 1898 (Key West)
Dermatolepis marmoratus Osburn and Mowbray, New York Zool.Soc.Publ., pp.1-3, 1915, (Key West).

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Labrus fulvus Linnaeus, Syst.Nat., ed.10, p.287, 1758 (after Catesby)
Epinephelus fulvus Jordan and Swain, Proc.U.S.Nat.Mus., vol.7, pp.402-5 1884
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Cephalopholis fulvus Jordan and Thompson, Bull.U.S.Bur. Fish., vol.24, (1904), p.239, 1905 (Tortugas)
Bodianus fulvus fulvus Nichols, Bull.Amer.Mus.Nat.Hist., vol.44, no.3, p.22, 1921 (Turks Island)
Cephalopholis fulvis Breder, Bull.Bingham Oceanogr.Coll., vol.1, no.1, p.39, 1927 (Royal Island, Swan Island)
Cephalopholis fulvus fulvus Fowler, Fish Cult., vol.21, p.68, 1942 (Cuba)
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Epinephelus punctatus Jordan and Gilbert, Bull.U.S.Nat.Mus., 16, p.541, 1883
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Bodianus fulvus var. punctatus Jordan and Eigenmann, Bull.U.S.Fish Comm., vol.8 (1888), p.380, 1890
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Bodianus fulvus punctatus Jordan and Evermann, Rept.U.S.Comm.Fish and Fish., vol.21 (1894-5), p.371, 1896

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Epinephelus (Bodianus) punctatus Metzelaar, Trop.Atl.Visschen, pp.46-7 1919 (Dutch West Indies)
Cephalopholis punctatus Fowler, Proc.Acad.Nat.Sci.Phila., vol.71, p.147, 1919 (Jamaica)
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Guativere Parra, Dif.Piezas Nat.Hist.Cuba.pp.7-8, pl.5, figs.1-2, 1787 (Havana)
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Serranus guativere Valenciennes, in Cuvier and Valenciennes, Hist.Nat. Poiss., vol.2, p.383, 1828
Enneacentrus punctatus var. guativere Goode, Amer.Jour.Sci.Arts, vol.14, p.292, 1877 (Bermuda)

Perca punctulata Gmelin, Syst.Nat.ed.13, p.1315, 1789
Sparus punctulatus Lacépède, Hist.Nat.Poiss., vol.4, p.155, 1802
Enneacentrus punctulatus Poey, Enumeratio, p.20-1, 1875 (Cuba)

Holocentrus auratus Bloch, Nat.Ausl.Fische, vol.4, p.75, pl.236, 1790
Serranus auratus Peters, Akad.Wissen.Berlin, Monatsb., (1865), p.103, 1866

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Petrometopon cruentatum (Lacépède)

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Petrometopon cruentatum coronatum Fowler, Proc.Acad.Nat.Sci., Phila., vol.59, p.252, 1907 (New Providence)

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Cephalopholis stellatus Jordan, Evermann and Clark, Rept.U.S.Fish.Comm. (1928) pt.2, p.309, 1930

Alphestes afer (Bloch) (Fig.4, p.1:27)

Epinephelus afer Bloch, Nat.Ausl.Fische, vol.7, p.12-3, pl.327, 1793 (Guinea, a doubtful locality)
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Prospinous chloropterus Poey, Repertorio, vol.2, p.289, 1868 (Cuba)
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Prospimus sp. Poey, Repertorio, vol.2, p.289, 1868
Serranus sp. Goode, Amr.Jour.Sci.Arts, vol.14, p.292, 1877 (Bermuda)
Dermatolepis inermis (not of Valenciennes) Bean, Field Col.Mus.Publ.108 (Zool.Series), vol.7, no.2, p.55, 1906
Epinephelus lightfooti Fowler, Proc.Acad.Nat.Sci.Phila., vol.59, pp.258-60, fig.3, 1907 (Santo Domingo)
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Alphestes fasciatus Hildebrand, Bull.U.S.Nat.Mus.189, pp.163-6, fig.36, 1946 (Perù)

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? Epinephelus apua Lee, Rept.U.S.Fish Comm., vol.14, (1886) p.671, 1889 (Nassau)
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Mycteroperca bonaci (Poey)

Bonaci arara Parra, Dif.Piezas Nat.Hist.Cuba, p.30, pl.16, fig.2, 1787 (Cuba)
Serranus arara Storer, Mem.Amer.Acad., vol.2, p.27, 1846 (after Parra, preoccupied by Serranus arara Valenciennes)

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Trisotropis tigris Poey, Ann.Lyc.Nat.Hist.New York, vol.9, p.307, 1870
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Mycteroperca tigris tigris Fowler, Fish Cult., vol.21, p.68, 1942 (Cuba)
Mycteroperca tigris Jordan, Proc.U.S.Nat.Mus., vol.9, p.39 (Havana, Cuba)
Epinephelus tigris Boulenger, Cat.Fishes. British Mus., ed.2, vol.1, pp.259-60, 1895
Serranus camelopardalis Poey, Memorias, vol.2, pp.132-4, 1860 (Cuba)
Trisotropis camelopardalis Poey, Repertorio, vol.2, p.283, 1868
Mycteroperca tigris var. camelopardalis Jordan and Swain, Proc.U.S.Nat. Mus., vol.7, p.364, 1884
Mycteroperca tigris camelopardalis Jordan, Proc.U.S.Nat.Mus., vol.9, p.39, 1886 (Havana)
Mycteroperca camelopardalis Jordan, Evermann and Clark, Rept.U.S.Fish. Comm., (1928) pt.2, p.315, 1930

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Trisotropis felinus Poey, Repertorio, vol.2, p.283, 1868
Serranus rivulatus Poey, Memorias, vol.2, p.135, 1860 (Cuba)
Serranus repandus Poey, Memorias, vol.2, pp.135-6, 1860 (Cuba)
Trisotropis reticulatus Gill, Proc.Acad.Nat.Sci.Phila., vol.17, p.105, 1865 (Barbados)
Mycteroperca reticulata Jordan and Swain, Proc.U.S.Nat.Mus., vol.7, p.373, 1884
Mycteroperca hopkinsi Jordan and Rutter, Proc.Acad.Nat.Sci.Phila., vol.49, p.105, 1897

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Serranus acutirostris Valenciennes, in Cuvier and Valenciennes, Hist.Nat. Poiss., vol.2, pp.286-7, 1828 (part)
Trisotropis microlepis Goode and Bean, Proc.U.S.Nat.Mus., vol.2, pp.141-3 1879 (Western Florida)
Epinephelus microlepis Jordan, Bull.U.S.Fish Comm., vol.4, p.77, 1884 (Key West)
Mycteroperca microlepis Jordan, Rept.U.S.Fish Comm., vol.13, p.872, 1885
Trisotropis brunneus (not of Poey) Goode and Bean, Proc.U.S.Nat.Mus., vol.2 p.143, 1879
Trisotropis stomias Goode and Bean, Proc.U.S.Nat.Mus., vol.5, p.427-8, 1882 (Pensacola)
Epinephelus stomias Jordan and Swain, Proc.U.S.Nat.Mus., vol.7, p.232 1884

Mycteroperca interstitialis (Poey) (Figs.4-5, pp.1:27-8)

Serranus interstitialis Poey, Memorias, vol.2, pp.127-9, 1860 (Cuba)
Trisotropis interstitialis Poey, Repertorio, vol.2, p.285, 1868
Mycteroperca interstitialis Jordan and Swain, Proc.U.S.Nat.Mus., vol.7 pp.365-6, 1884
Epinephelus (Mycteroperca) interstitialis Metzelaar, Trop.Atl.Visschen p.51, fig.19, 1919 (Guanta, Venezuela)
Serranus dimidiatus Poey, Memorias, vol.2, p.129, 1860 (Cuba)
Trisotropis dimidiatus Poey, Repertorio, vol.2, p.285, 1868
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Epinephelus dimidiatus Boulenger, Cat.Fishes British Mus., ed.2, vol.1, pp.264-5, 1895
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Trisotropis falcatus Poey, Repertorio, vol.2, p.285, 1868

Epinephelus falcatus Boulenger, Cat.Fishes British Mus., ed.2, vol.1, pp.261-2, 1895
Mycteroperca falcata var. falcata Jordan and Swain, Proc.U.S.Nat.Mus., vol.7, pp.362-3, 1884
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Mycteroperca falcata falcata Breder, Field Book Marine Fishes, p.161, 1929
Mycteroperca calliura Poey, Repertorio, vol.1, pp.181-3, 1867 (Cuba)
Trisotropis calliurus Poey, Repertorio, vol.2, p.284, 1868
Epinephelus calliurus Boulenger, Cat.Fishes British Mus., ed.2, vol.1, p.264, 1895
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Trisotropis sp. Poey, Enumeratio, p.14, 1875
? Mycteroperca roquensis Martin-S., Ictiol.del Arch.d.l.Roquas, pp.100-2, 1956 (Gran Roque, Venezuela)

Mycteroperca phenax Jordan and Swain (Fig.5, p.1:28)

Trisotropis falcatus (not of Poey) Goode and Bean, Proc.U.S.Nat.Mus., vol.2 pp.141-2, 1879 (Pensacola, Florida)
Epinephelus falcatus Jordan, Bull.U.S.Fish Comm., vol.4, p.77, 1884
Mycteroperca falcata Henshall, Bull.U.S.Fish.Comm., vol.14 (1894) p.215 1895
Mycteroperca falcata phenax Jordan and Swain, Proc.U.S.Nat.Mus., vol.7, pp.363-4, 1884
Mycteroperca phenax Jordan, Evermann and Clark, Rept.U.S.Fish Comm., (1928) pt.2, p.315, 1930
Mycteroperca interstitialis (not of Poey) Kendall, Occ.Paps.Boston Soc.Nat. Hist., vol.7, p.99, 1908 (Katama Bay)
Mycteroperca venenosa Smith, Bull.U.S.Fish Comm., vol.21, (1901), p.33, 1902 (Woods Hole)

Mycteroperca rubra (Bloch) (Fig.5, p.1:28)

Epinephelus ruber Bloch, Nat.Ausl.Fische, vol.7, pp.22-3, pl.331, 1793
Serranus ruber Peters, Monatsber.Akad.Wissen. Berlin (1865) p.107, 1866
Mycteroperca rubra Jordan and Eigenmann, Bull.U.S.Fish Comm., vol.8 (1888) pp.372-4, 1890
Epinephelus (Mycteroperca) ruber Metzelaar, Trop.Atl.Visschen,pp.51-2 1919 (Venezuela)
Serranus acutirostris (part) Valenciennes, in Cuvier and Valenciennes, Hist. Nat.Poiss., vol.2, pp.286-7, 1828
Trisotropis acutirostris Goode and Bean, Proc.U.S.Nat.Mus., vol.2, p.143, 1879

Mycteroperca acutirostris Fowler, Proc.Acad.Nat.Sci.Phila., vol.59 p.261, 1907

Parepinephelus acutirostris Bleeker, Archiv.Neer.des Sci.Exet. (1875), p.257, 1876

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Serranus undulosus Valenciennes, in Cuvier and Valenciennes, Hist.Nat.Poiss., vol.2, p.295, 1828 (Brazil)

Trisotropis undulosus Poey, Ann.Lyc.Nat.Hist.New York, vol.9, p.305 1870

Serranus fuscus Lowe, Trans.Cambridge Philos.Soc. vol.6, p.196, 1838

Serranus emarginatus Valenciennes, Ichth.Iles Canaries, p.10, 1839

Epinephelus chalinius Cope, Trans.Amer.Philos.Soc., vol.14, pp.465-6, 1871 (St. Martins)

? Mycteroperca scirenga (not of Rafinesque) Jordan and Swain, Proc.U.S.Nat. Mus., vol.7, pp.369-70, 1884

1.2.3 Standard common names, vernacular names

Scientific names	Standard common names	Vernacular names
Paranthias furcifer	Barber	Creole fish
Epinephelus striatus	Nassau Grouper	Hamlet
E. morio	Red Grouper	
E. guttatus	Red Hind	
E. drummondhayi	Speckled Hind	
E. niveatus	Snowy Grouper	
E. flavolimbatus	Yellowedge Grouper	
E. nigritus	Warsaw	
E. mystacinus	Misty Grouper	
E. adscensionis	Rock Hind	
E. itajara	Jewfish	
E. guaza	—	
Dermatolepis inermis	Marbled Grouper	
Cephalopholis fulva	Coney	
Petrometopon cruentatum	Graysby	
Alphestes afer	Mutton Hamlet	
Mycteroperca venenosa	Yellowfin Grouper	
M. bonaci	Black Grouper	
M. tigris	Tiger Grouper	
M. microlepis	Gag	
M. interstitialis	Yellowmouth Grouper	
M. phenax	Scamp	
M. rubra	—	

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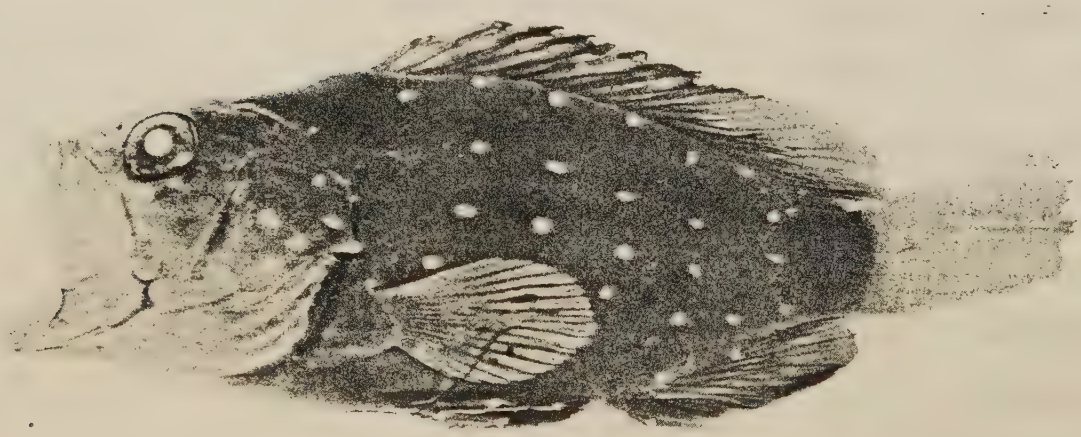

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Fig. 1 1. Epinephelus striatus 45.6 mm, Bermuda
2. E. guttatus 130 mm, Bermuda
3. E. niveatus 66,5 mm, Woods Hole, Massachusetts

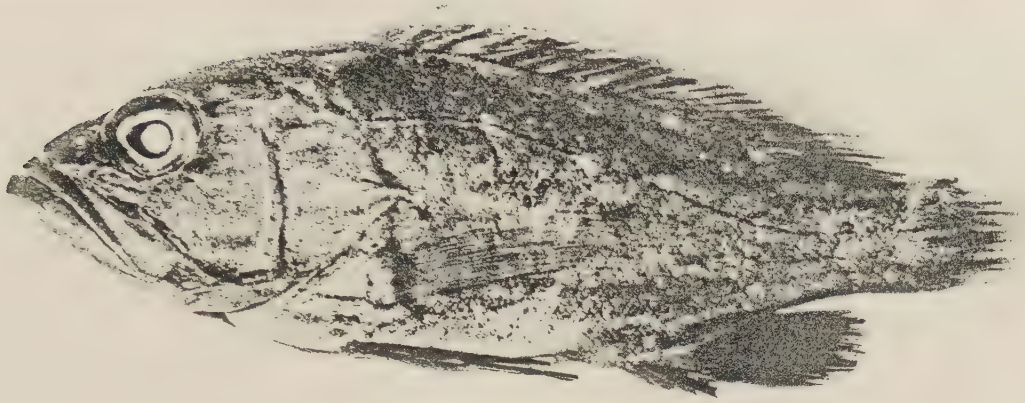

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Fig. 2 1. Epinephelus flavolimbatus 134 mm, Tortugas, Florida
2. E. nigritus 78 mm, Katuma Bay, Massachusetts
3. E. adscensionis 76 mm, from Bimini, Bahama Isle

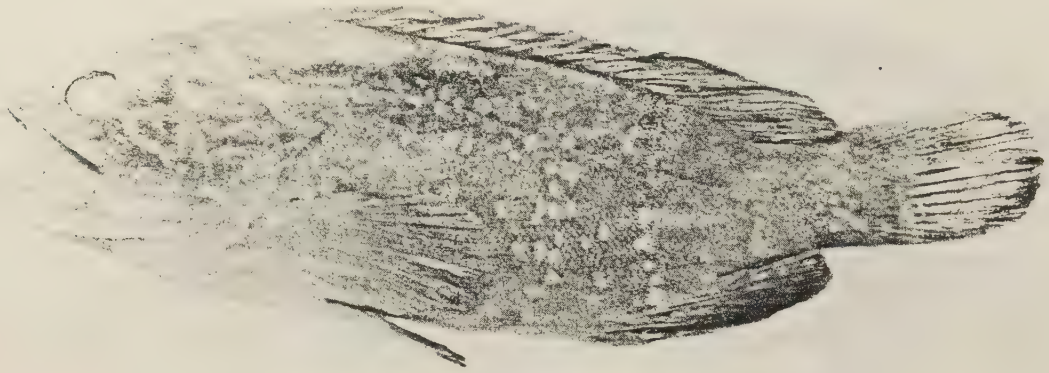

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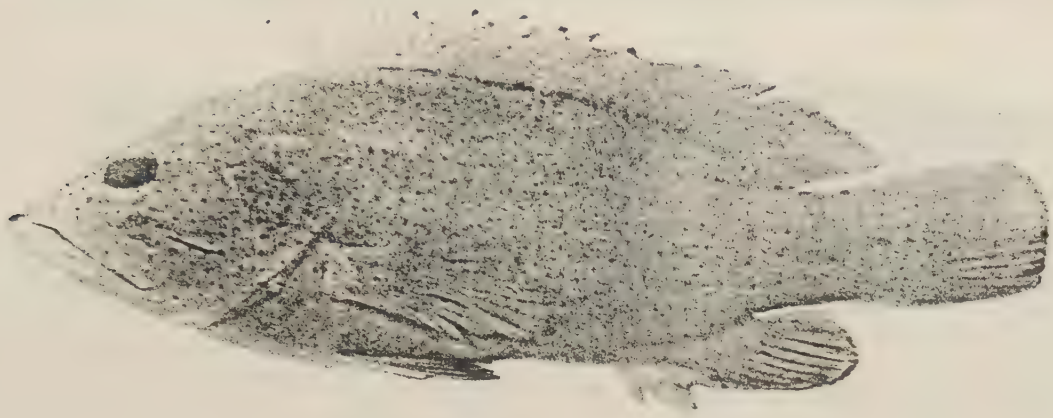
Fig. 3 1. Epinephelus guaza 205 mm, Rio de Janeiro, Brazil
2. Dermatolepis inermis 214 mm, from Miami, Florida
3. Cephalopholis fulva 200 mm, Golden form from Bermuda



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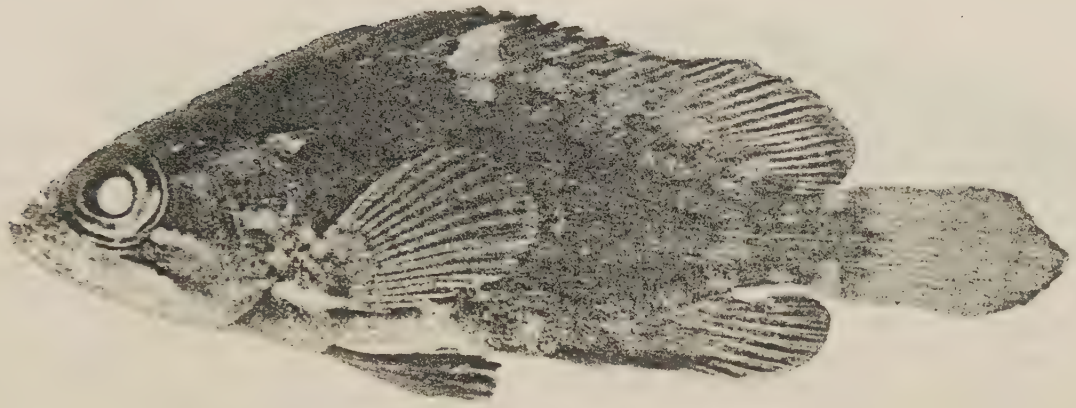

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Fig. 4 1. Cephalopholis fulva 190 mm, deepwater red form from Bermuda
2. Alphestes afer 37.5 mm, Bermuda
3. Mycteroperca interstitialis 37.4 mm, bicolored juvenile from Bermuda

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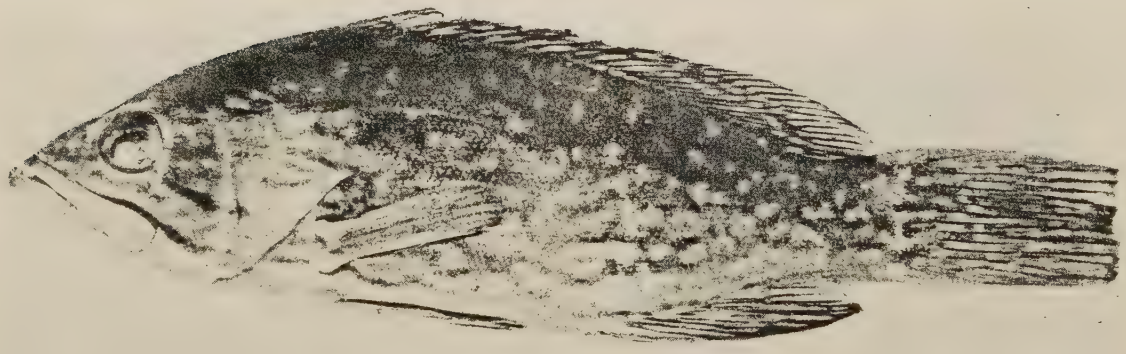

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Fig. 5 1. Mycteroperca interstitialis 107 mm, Bermuda
2. M. phenax 220 mm, Miami, Florida
3. M. rubra 12.8 mm, Rio de Janeiro, Brazil

1.3 General variability

1.3.1 Subspecific fragmentation (races, varieties, hybrids)

At present there are no infraspecific units recognized within any species of grouper known from the western Atlantic region. This, however, may merely be a reflection of a lack of study for there have been no recent investigations of geographic variation within any single species and museums do not now have sufficiently representative collections of specimens to permit such studies. Survey studies by the author (unpublished dissertation, University of Michigan, 1959) indicate considerable variation in morphometric features while meristic characters show little intraspecific variation. Perhaps the best taxonomic characters of these fishes are features of coloration - shade and hue as well as pattern. Groupers exhibit a wide spectrum of individual color variations and this has led to much confusion but once these variations and their limits are understood most species are readily identified on the basis of color characters.

Color phases in groupers fall into three categories. First there is the "instantaneous" color change which is under direct nervous and hormonal control. These changes occur with striking rapidity in the individual fish. The Nassau grouper, Epinephelus striatus can change in seconds from a nearly uniform dark brown to a very pale gray, or to a striking barred pattern. The coney Cephalopholis fulva, has an "excitement phase" in which the body is sharply bicolored, dark brown above and creamy white below. This pattern is assumed when the fish is alarmed or when the presence of food stimulates it to activity and stands in stark contrast to the usual nearly uniform ground color of resting fish. At night, when at rest and under other conditions, some groupers and many other reef fishes assume a pattern of irregular bars and dark blotches. This is termed the "sleep" pattern but may be considered as a special case of istantaneous variation. This ability to undergo rapid color changes is developed in varying degrees in all of the groupers which the author has been able to observe alive.

The second type of color variation is an environmental effect which has led to some taxonomic confusion. Like many other shore fishes having a considerable vertical range, groupers which are taken in deeper water tend to be more red than individuals of the same species captured in shallow water. In a few species (Mycteroperca venenosa, Cephalopholis fulva, Petrometopon cruentatum) the difference, which involves a loss of melanin as well as an increase in carotenoids, is so striking that the deep and shallow water forms have been named as distinct species or subspecies. In view of the perfect intergradation and close correlation with depth it seems that these bathymetric forms are probably not genetically distinct.

These first two types of color variation are superimposed on the third type, the individual, presumably genetic, color pattern. Variations in color pattern

are most readily noted in those species which are spotted where probably no two individuals ever have patterns exactly alike. Such variations although subtle, may prove of value in future racial studies.

Among the Atlantic groupers Cephalopholis fulva has a xanthic phase which makes up a small proportion of the population. These yellow individuals are found in deep and shallow waters and appear to be the result of one or a few genes. When adequate collecting or census methods are available the frequency of this xanthic form may be of value in racial studies in the same way that blood group frequencies are used in distinguishing human populations.

Only one hybrid combination has come to the attention of the writer. This is the combination Cephalopholis fulva X Paranthias furcifer known from two specimens in the Museum of Comparative Zoology of Harvard University. These specimens are from the vicinity of Havana, Cuba and form the types of Menephorus dubius and Menephorus punctiferus described by Poey (Memorias vol.2, p.142-3, 1860; Enumerat. p.21-2, 1875). The hybrids are intermediate in 40 or 45 features studied including counts, measurements, and color characters. They fall within the range of one or both parents in the other 5 characters (Smith, op.cit.). This hybrid combination is a particularly easy one to trace, for of the western Atlantic groupers only Cephalopholis fulva has guanoiridiophores of the type present in the hybrid, and only Paranthias has a deeply forked tail (the tails of the hybrid being moderately forked). This is the chief reason why Paranthias furcifer is considered a grouper although one extreme in many characters.

2 DISTRIBUTION

2.1 Delimitation of the total area of distribution and ecological characterization of this area

The distribution of the groupers of the western north Atlantic corresponds roughly to the distribution of the reef building corals, i.e. their northern limit is approximately represented by the extended 70°F isotherm. They are also confined to relatively shallow waters as are the corals. Although not all grouper species are confined to the coral reef environment most of them seldom stray far from shelter of some kind and the coral areas seem to be optimum. The ability to undergo rapid color change may have special significance among the bright colors of the coral reefs. The groupers here considered seldom if ever enter fresh or brackish water but this is perhaps more closely correlated with the lack of hard substrate in estuarine situations than with salinity conditions for Townsend (1905:101) reported that Nassau groupers (Epinephelus striatus) lived for several years in the old New York aquarium in water which at times became nearly fresh and was frequently quite polluted. Although groupers are pantropical in their distribution individual species have restricted geographic ranges. The accompanying distribution maps show the locality records of all of the western Atlantic groupers except Epinephelus guaza which is known from only a few localities. (see figs.6 to 19, pp.2:3 to 2:16)

These distribution maps are taken from an unpublished dissertation by the author. They include published records as well as the localities from which he has examined specimens. Some species not found in the western North Atlantic appear on these maps but they have not been discussed in the text. The records for these eastern Pacific species are incomplete as the author has not examined many recent collections which are in west coast museums. Localities that fall beyond the limits of the base maps are listed in the legends. Doubtful locality records have been eliminated.

Solid symbols on the maps indicate localities from which the author has seen specimens; open symbols indicate literature records.

Of the genera found in western north Atlantic waters Epinephelus, Cephalopholis, Petrometopon, and Dermatolepis have representatives in the Indo-Pacific fauna while Mycteroperca, Alphestes and Paranthias appear to be confined to the American fauna (Atlantic and eastern Pacific oceans). Epinephelus guaza, Mycteroperca rubra, and Paranthias furcifer have representative populations in the eastern Atlantic and Paranthias furcifer, Alphestes afer, Epinephelus niveatus, and E. itajara have eastern Pacific populations which seem to be indistinguishable from the Atlantic forms, at least at the species level.

2.2 Differential distribution

2.2.1 Areas occupied by eggs, larvae and other junior stages: annual variations in these patterns, and seasonal variations for stages persisting over two or more seasons. Areas occupied by adult stages: seasonal and annual variations of these.

At present there is so little information available on the distribution of young stages of groupers that no concise statements can be made about the area occupied by these stages. It is apparent, however, that young of the year groupers have a somewhat wider distribution than do the adults. Small specimens of Epinephelus niveatus, E. nigritus, Mycteroperca phenax, and M. microlepis, presumably young of the year, have been taken as far north as Woods Hole, Massachusetts, but the adults of these species are rare or absent north of the Carolinas. This appears to be a natural result of a pelagic larval existence; the young are swept far out of the normal range of the adults and under the proper conditions may find a tolerable habitat in which they can survive and grow only during the warmer months.

2.3 Behaviouristic and ecological determinants of the general limits of distribution and of the variations of these limits and of differential distribution

Probably the greatest factor in the behaviour of groupers is their need for shelter - crevices and holes in which to hide. Stereotropism is strong in most species and specimens observed in captivity spent nearly all of their time in contact with the bottom or sides of the aquaria in which they were kept. Field observations suggest that most species seldom stray far from shelter. Some groupers will dart to the surface to take a lure trolled over them, but they generally shun the mid-depths and remain near the bottom. There is some indication that individual groupers are confined to rather narrow depth ranges as adults. Perhaps the best evidence for this is the development of definite bathymetric color phases in some species. Experiments conducted at the Bermuda Biological Station by Dr. John Bardach indicate that several weeks are required to change the coloration of a given individual fish. Thus, if the fish moved through various depths indiscriminately, they would not have time to assume these depth correlated colors (Bardach, in litt.). Another behaviouristic factor in the determination of the range of the adults is that groupers have a strong homing tendency, thus their emigration to remote places must be accomplished chiefly during the pelagic larval stages and is closely dependent upon ocean currents. Another important factor in the general distribution of groupers is probably temperature although tolerance limits have not been reported.

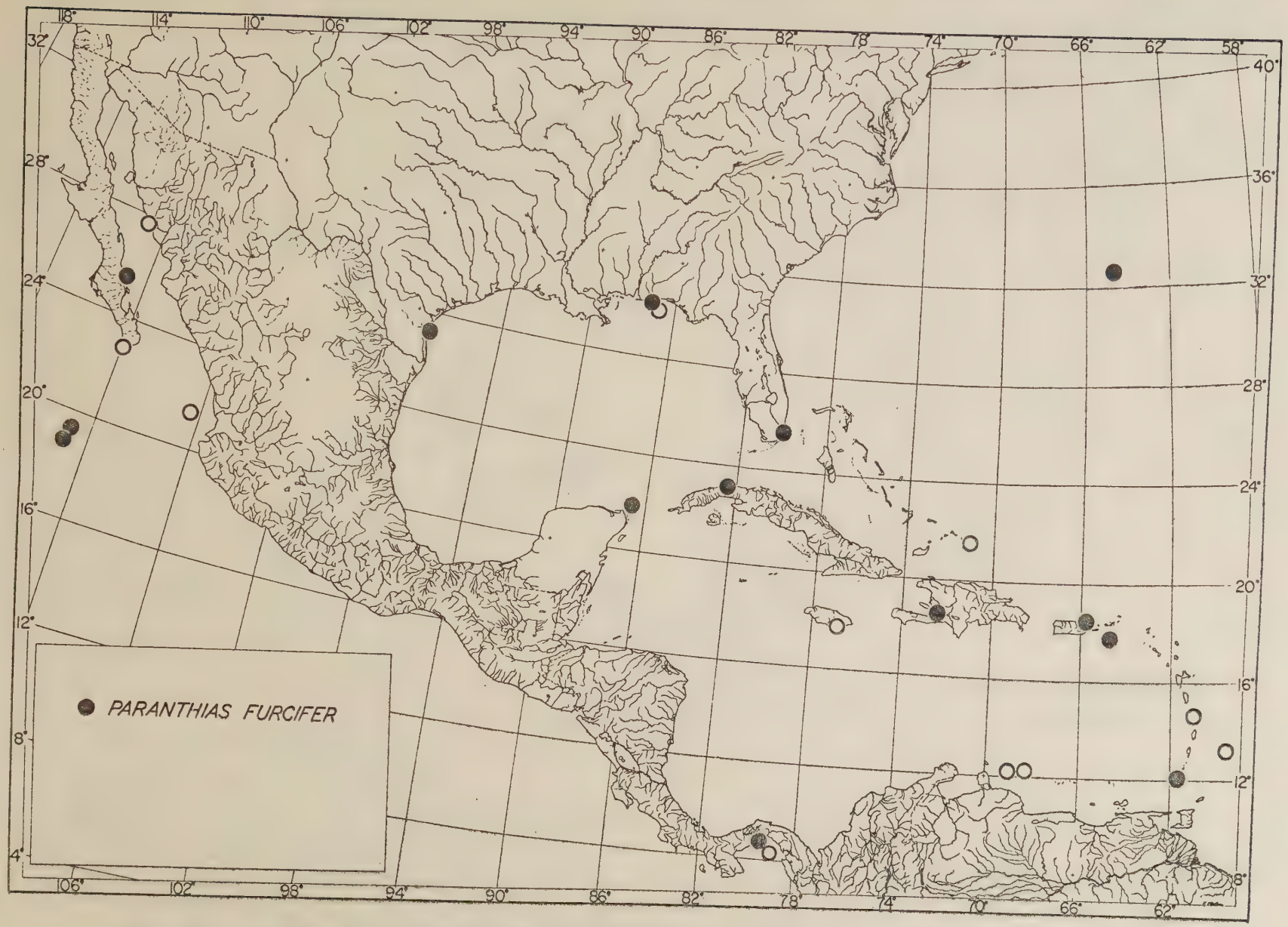

Fig. 6 Some record stations for Paranthias furcifer

Additional specimens were examined as follows: Atlantic - Rio de Janeiro; Pacific - Clarion Islands, Cocos Island, Galapagos Islands, Lobos de Afuera, Peru. Additional literature records are from the west coast of Africa and Fernando de Noronha.

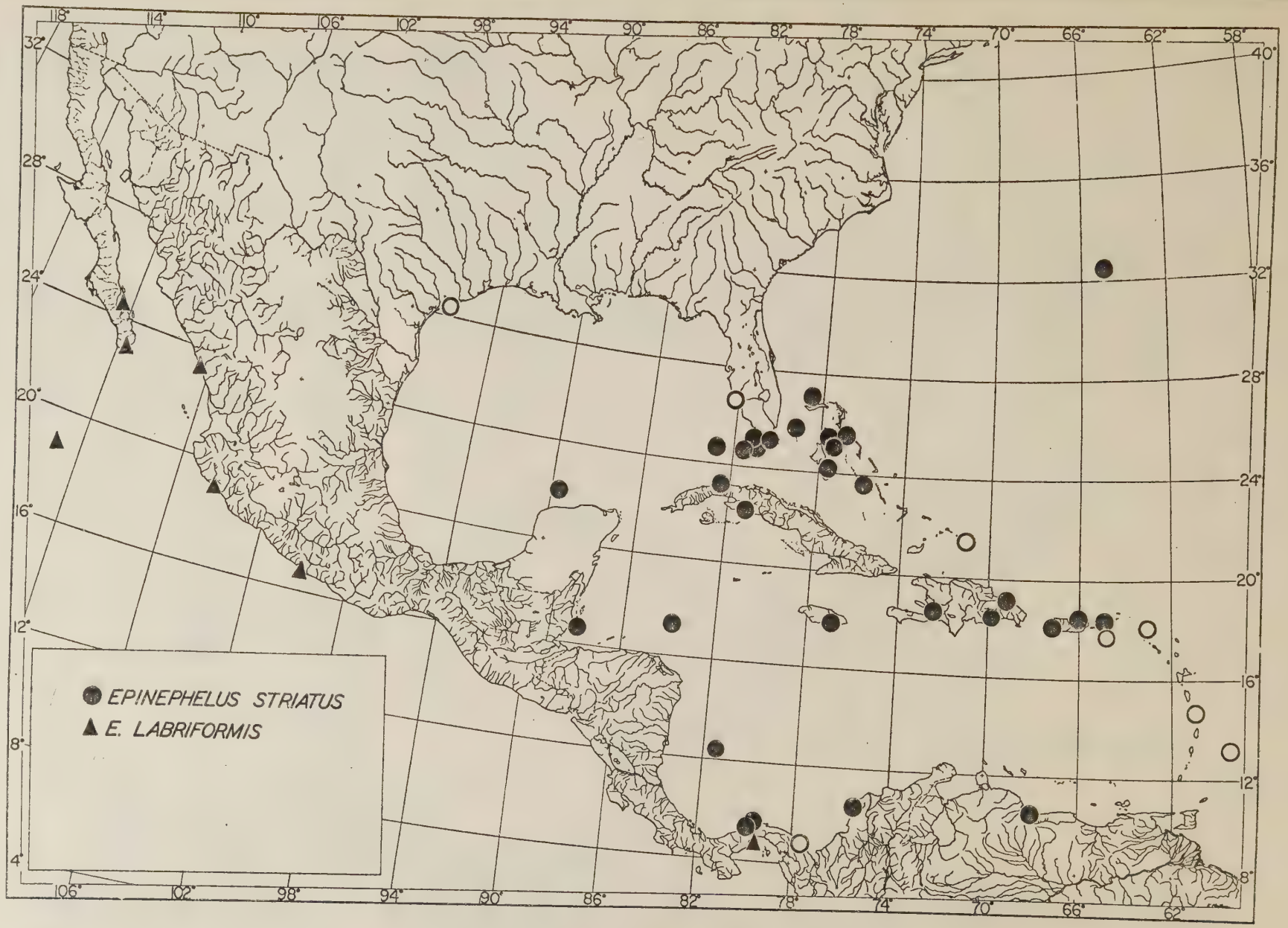

Fig. 7 Some record stations for Epinephelus striatus and E. labriformis

There are additional records of Epinephelus labriformis from Clarion Island, Cocos Island, Galapagos Islands, and Peru.

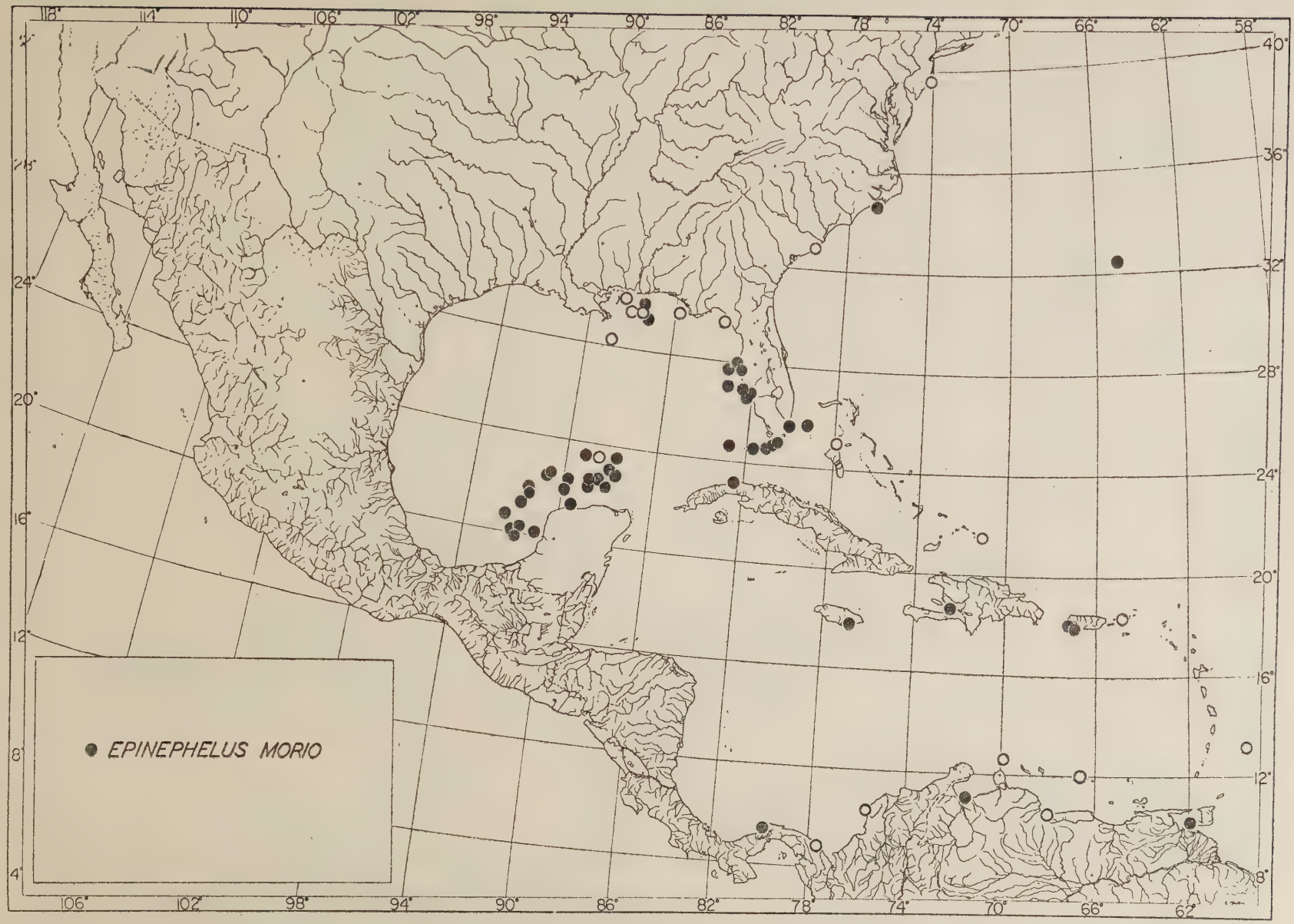

Fig. 8 Some record stations for Epinephelus morio

Specimens from Brazil were examined and there are literature records from Katama Bay, Mass., and Para, Bahia, and Rio de Janeiro, Brazil. The species has also been reported from the Texas coast.

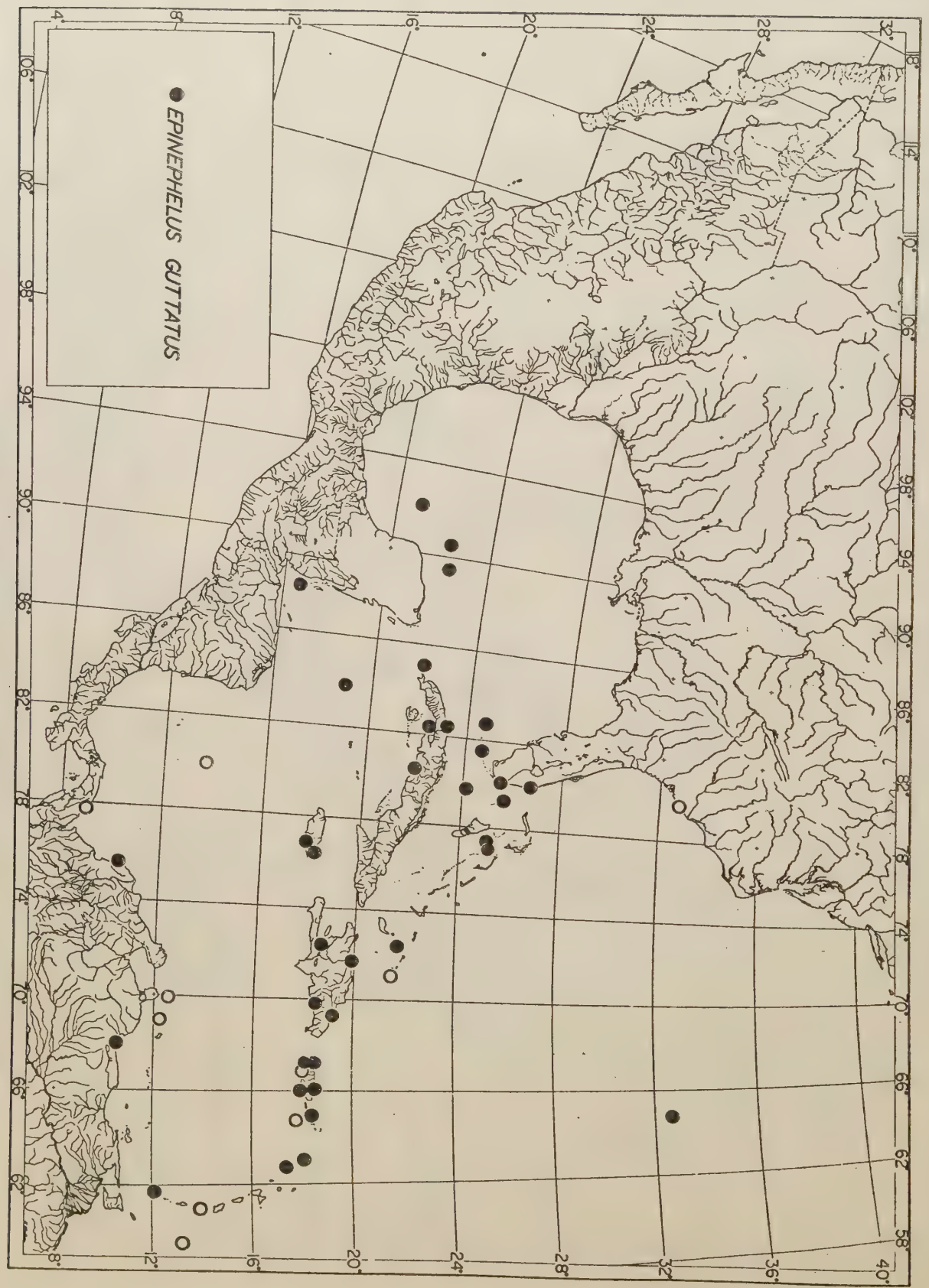

Fig. 9 Some record stations for Epinephelus guttatus

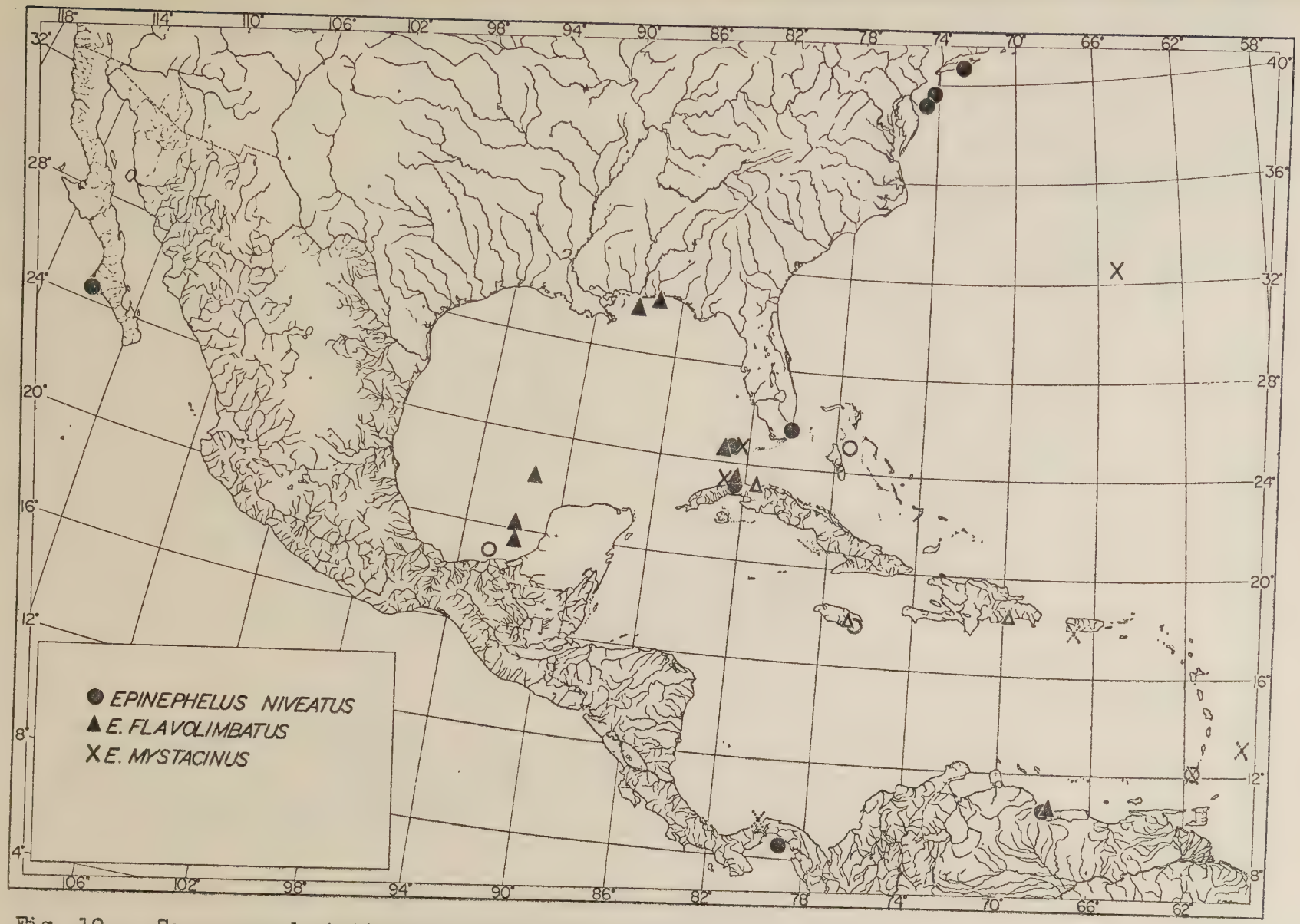

Fig. 10 Some record stations for Epinephelus niveatus, E. flavolimbatus, and E. mystacinus

Additional specimens of Epinephelus niveatus were examined from Katama Bay, Mass., Port Judith, R.I., and Rio de Janeiro. There are additional literature records from Newport, R.I., and Rio Grande do Sul.

The author has examined additional specimens of Epinephelus flavolimbatus from Brazil, and Surinam (06°50'N., 54°04'W.)

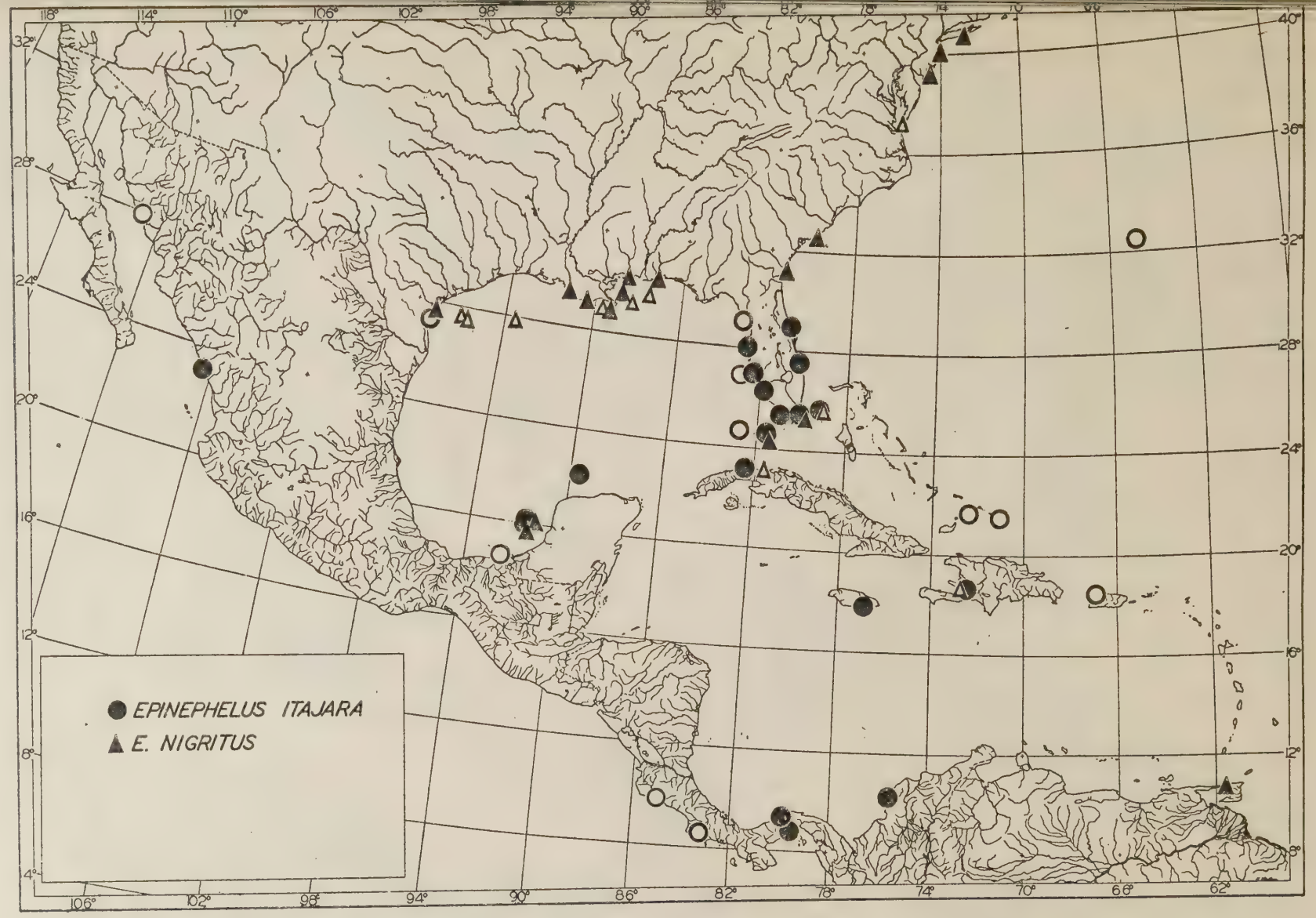

Fig. 11 Some record stations for Epinephelus itajara and E. nigritus

Additional specimens of Epinephelus itajara were examined from Maceio, Recife Pernambuco, Bahia, and Rio de Janeiro, Brazil. Literature records of the same species which are not shown on the map are from British and Dutch Guiana, the Pacific coast of Guatemala, and Callao, Perù.

Epinephelus nigritus specimens were also seen from Katama Bay, Mass., Port Judith, R.I., and Rio de Janeiro, Brazil. Additional literature records of this species are from Block Island, Cuba, and Rio Grande do Sul.

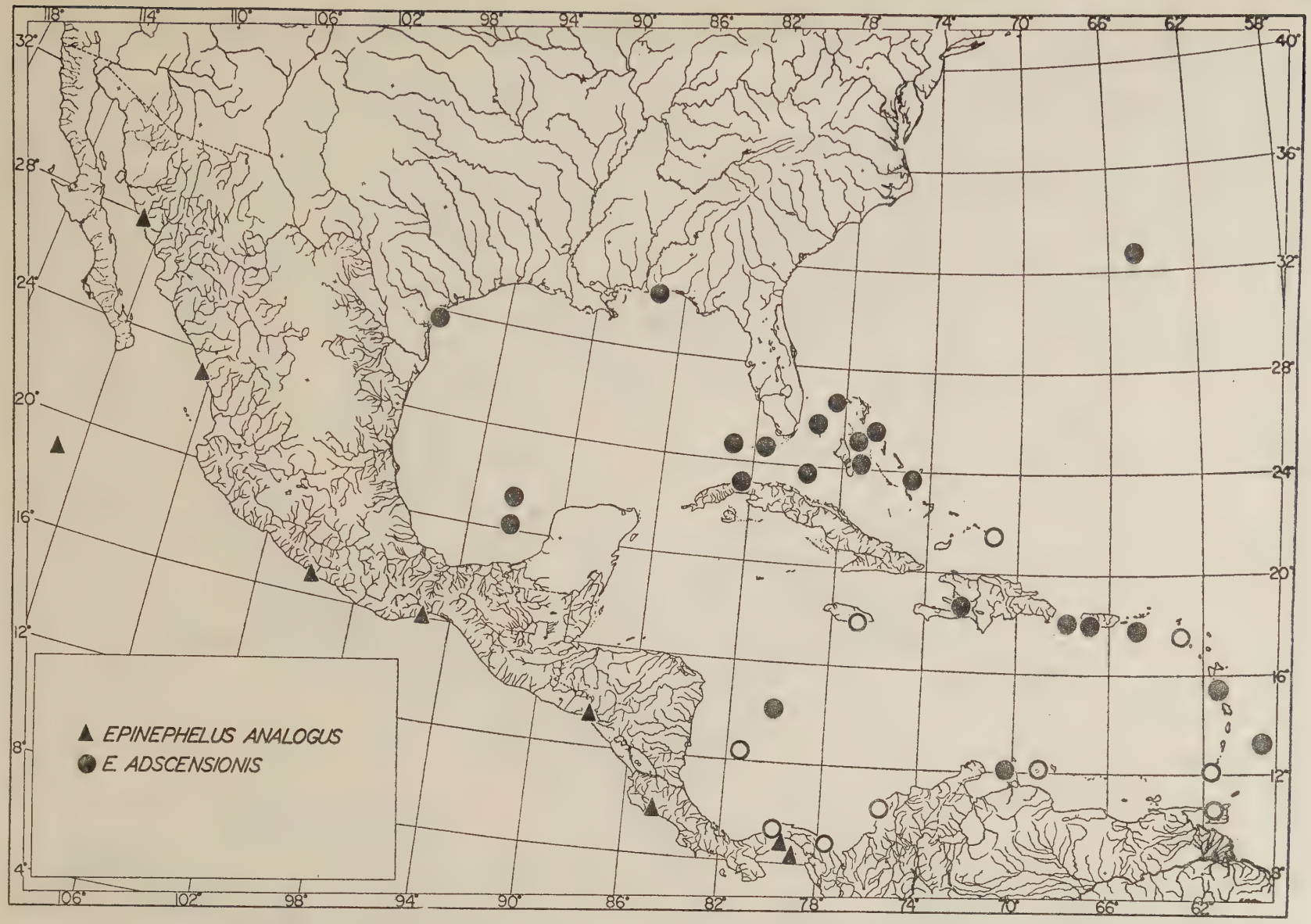

Fig. 12 Some record stations for Epinephelus analogus and E. adscensionis

There are additional literature records for Epinephelus analogus from Clarion Island, Jalisco, and Charles Island in the Galapagos.

Other specimens of Epinephelus adscensionis were examined from Maceio, Recife Pernambuco, Rio Grande do Sul, and Rio de Janeiro, Brazil. Additional literature records for this species are from Ascension Island, St. Helena, Cape Verde Islands, South Trinidad Islet, South Africa, and Bahia, Brazil.

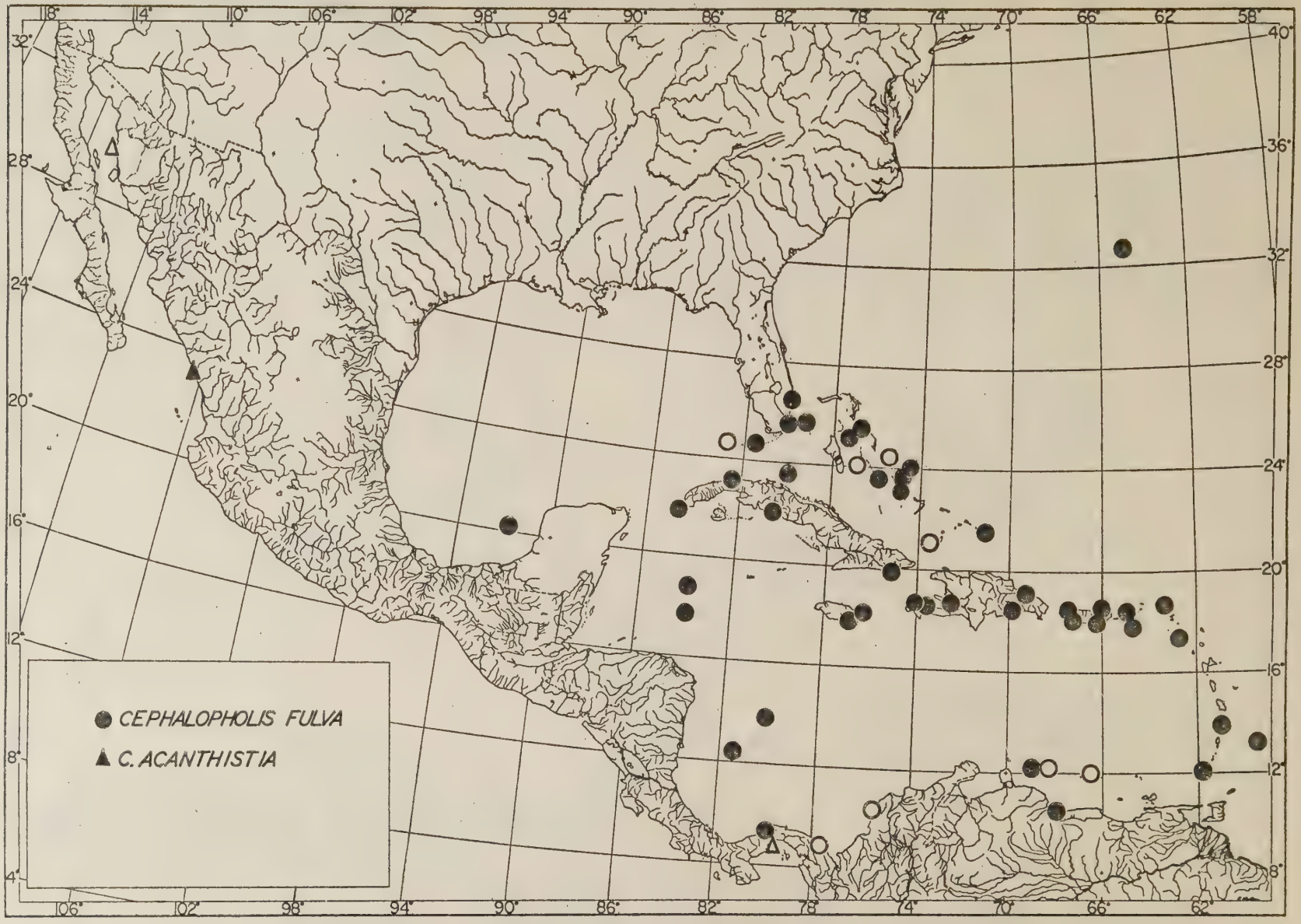

Fig. 13 Some record stations for Cephalopholis fulva and C. acanthistia

Other localities from which specimens of Cephalopholis fulva were examined are Bahia, Maranhao, and Rio de Janeiro, Brazil. Additional literature records for this species are from Natal and Pernambuco, Brazil

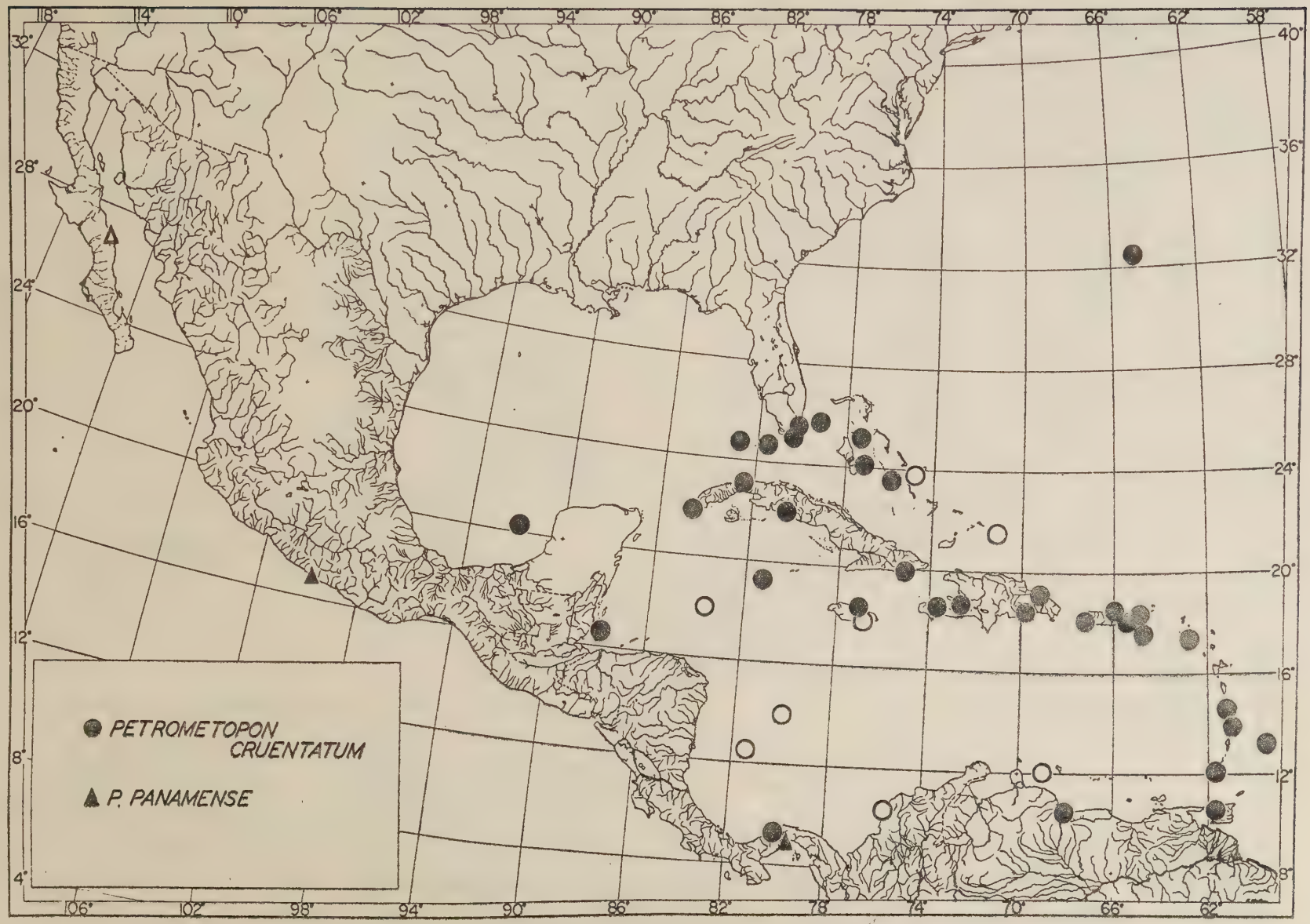

Fig. 14 Some record stations for Petrometopon cruentatum and P. panamense

Additional specimens of Petrometopon panamense were examined from Puerto Marquez Bay, Mexico, Puerto Refugio, Gulf of California, and Gorgona Island, Colombia.

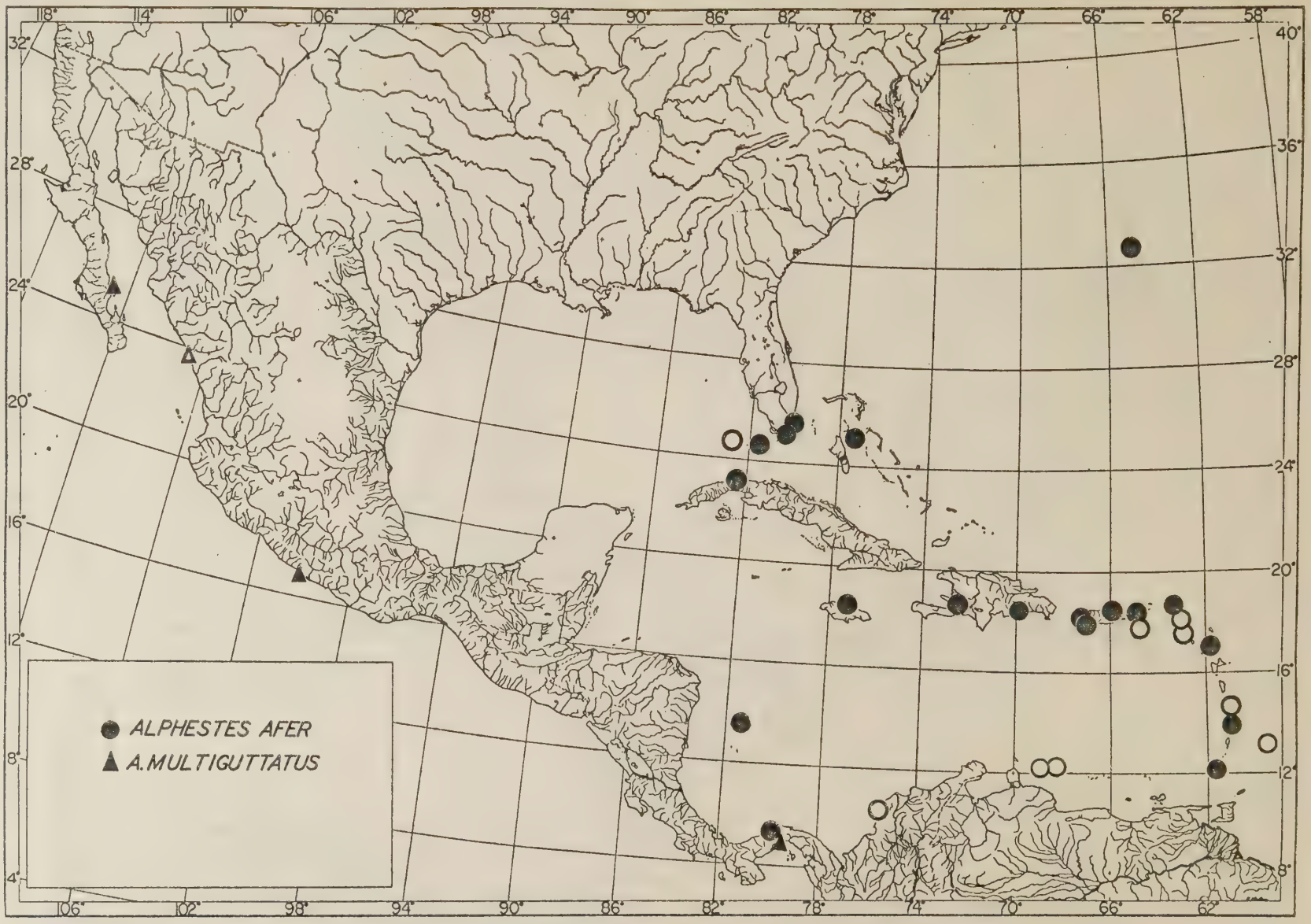

Fig. 15 Some record stations for Alphestes afer and A. multiguttatus

Additional specimens of Alphestes afer have been examined from Bahia and Recife Pernambuco, Brazil in the Atlantic, and the Galapagos Islands and Perù in the Pacific.

Alphestes multiguttatus literature records not shown are James Island in the Galapagos, Pearl Islands, and Jalisco, Mexico.

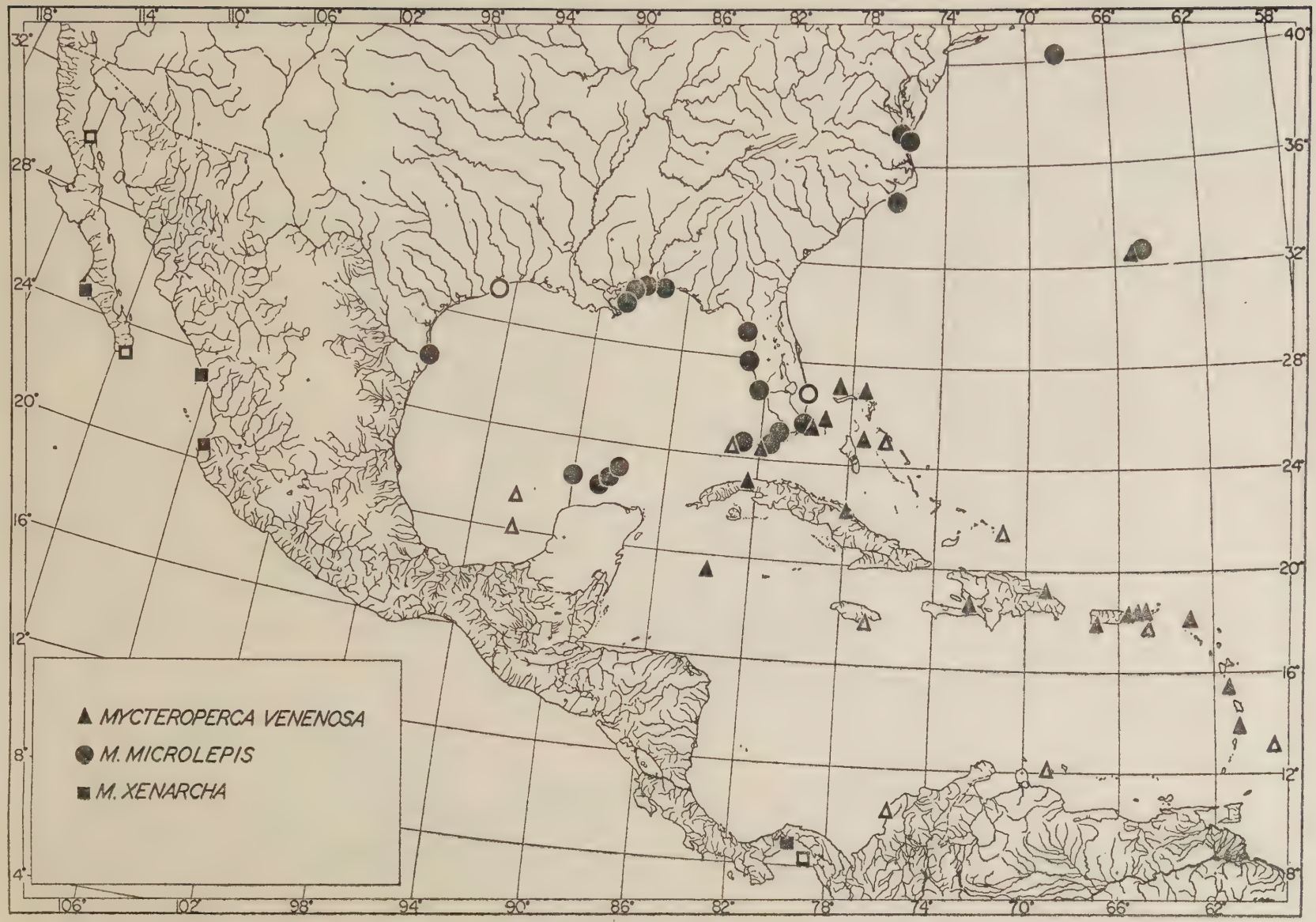

Fig. 16 Some record stations for Mycteroperca venenosa, M. microlepis and M. xenarcha

Specimens of Mycteroperca venenosa were also examined from Maranhão, Brazil. Another specimen of Mycteroperca microlepis came from Rio de Janeiro. There are literature records of Mycteroperca xenarcha from James Island in the Galapagos,

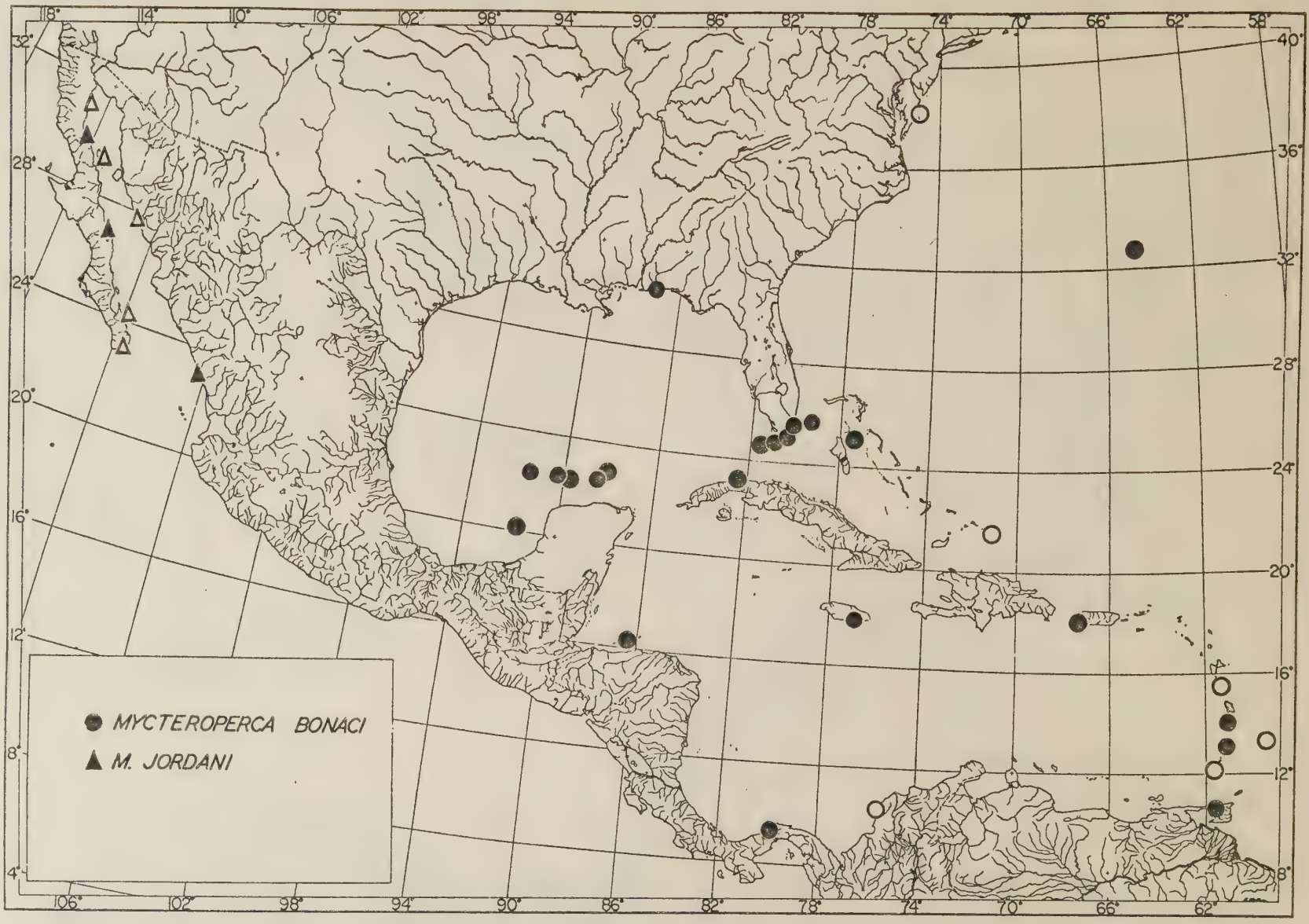

Fig. 17 Some record stations for Mycteroperca jordani and M. bonaci

Additional records of Mycteroperca bonaci supported by specimens are from Rio de Janeiro and there are literature records from Surinam and from Woods Hole, Mass.

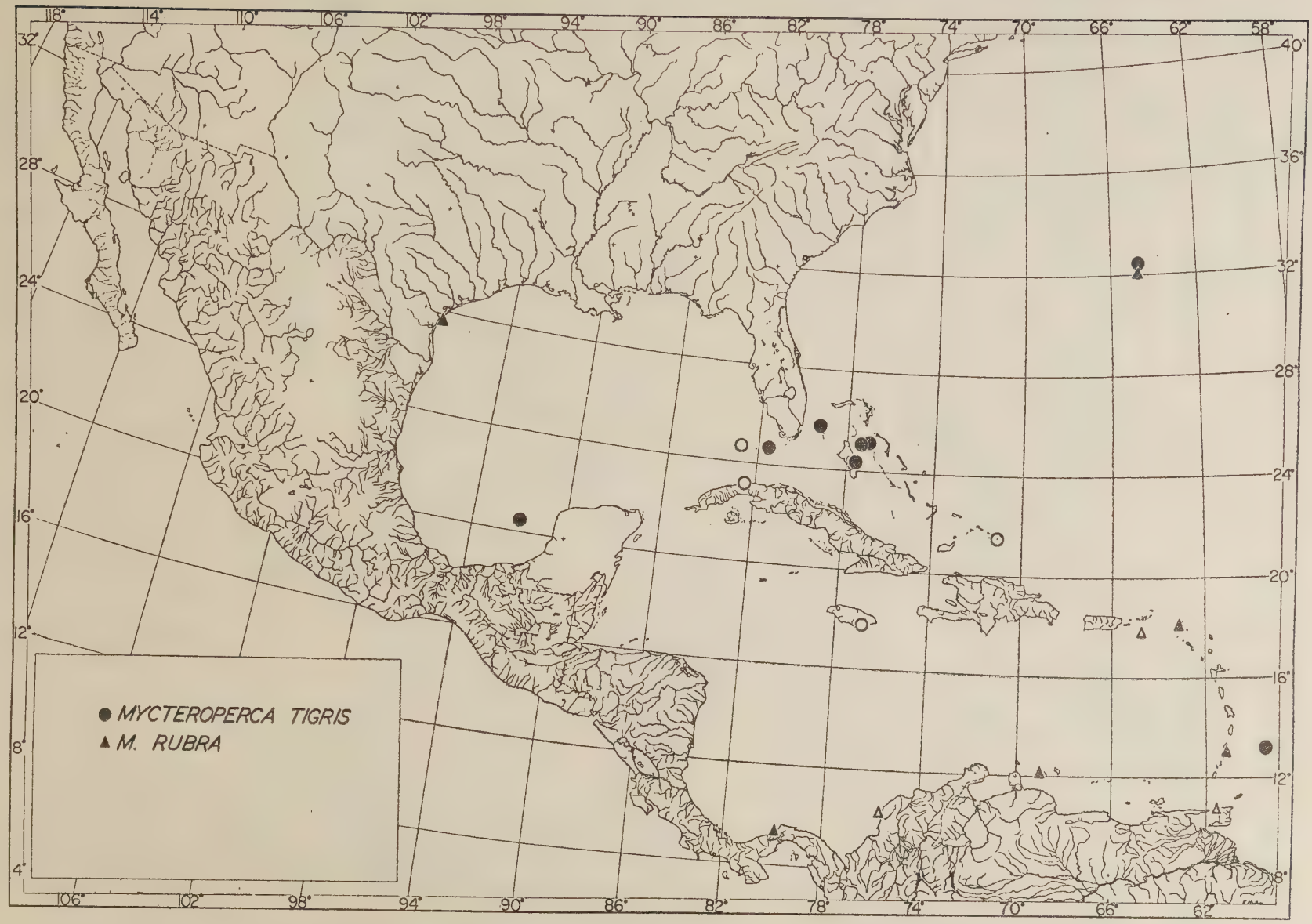

Fig. 18 Some record stations for Mycteroperca tigris and M. rubra

Mycteroperca tigris has been reported from Maranhão, Brazil in addition to the localities shown on the map. Additional Western Atlantic records of Mycteroperca rubra are from Santos and Rio de Janeiro, Brazil.

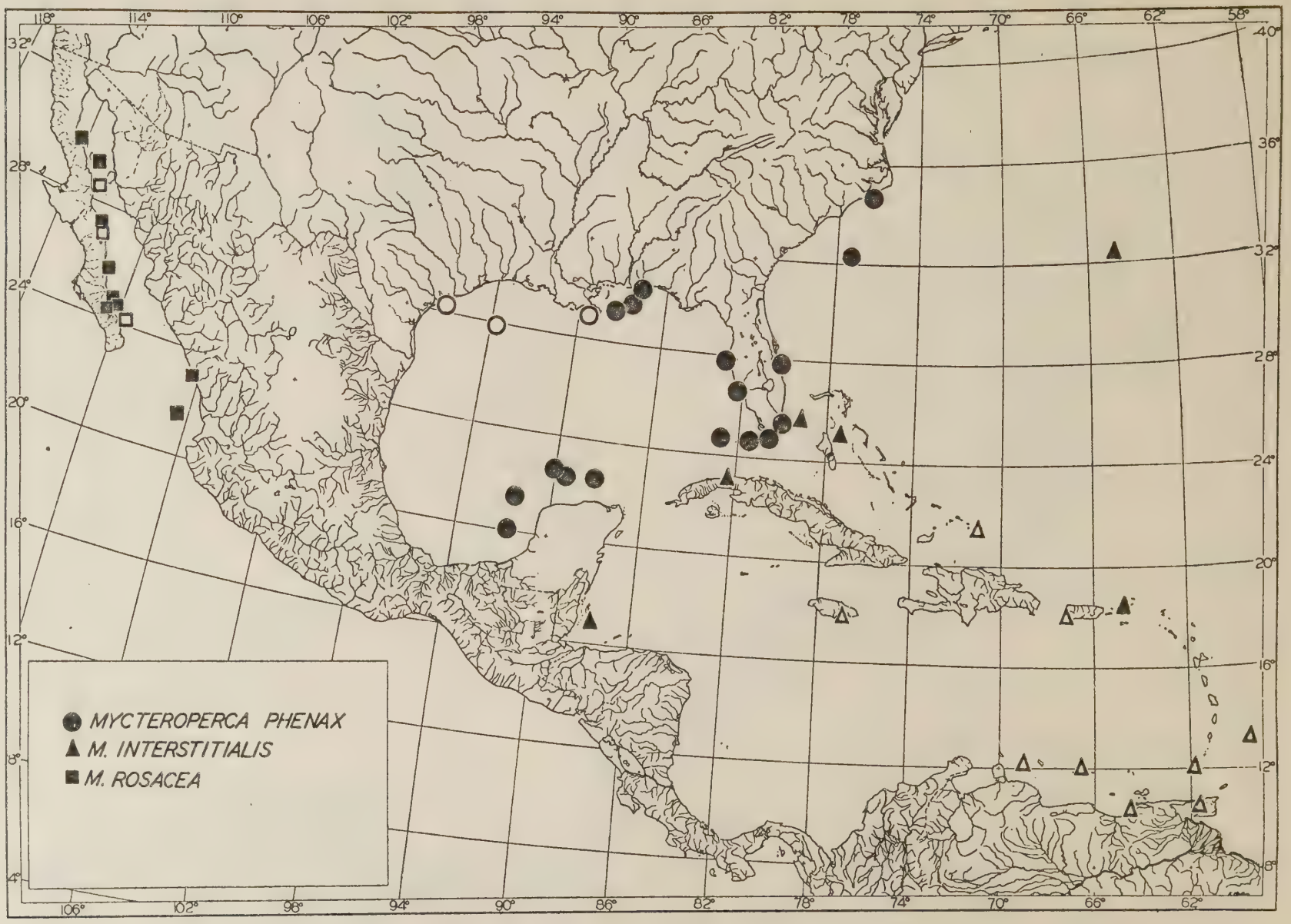

Fig. 19 Some record stations for Mycteroperca phenax, M. interstitialis and M. rosacea

A specimen of Mycteroperca phenax was examined from Woods Hole, Mass., and a specimen of M. interstitialis from Bahia, Brazil

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality (Hermaphroditism, heterosexuality, intersexuality)

Smith (1959) presented evidence that most species of groupers are proterogynous hermaphrodites. This conclusion was based on histological and field evidence and corroborated Lavenda's (1949) findings on the Black Sea Bass (Centropristes striatus Linn.). The following species were studied and definite or strongly suggestive indications of sex reversal were obtained in each case: Epinephelus striatus, E. guttatus, E. itajara, Cephalopholis fulva, Petrometopon cruentatum, Alphestes afer, Mycteroperca venenosa, M. bonaci, M. tigris, M. interstitialis. The results were inconclusive in the case of Paranthias furcifer and that species may well be gonochoritic. Evidence of the proterogynous condition was as follows:
(1) No small males were found even when gonads were examined histologically.
(2) With increasing size of mature fish the proportion of males increased. In nearly all species examined the largest fish were males. (3) All of the testes examined histologically contained remnants of degenerating oocytes. In most cases these were oocytes which had developed egg membranes.

3.1.2 Maturity (age and size)

There is a strong suggestion that several seasons may be spent as functional females before the sex reversal occurs, but reliable aging techniques have not been worked out for these tropical and subtropical fishes, hence data on age and size at maturity are not available. Some indication of the size at maturity and sex reversal may be gained from Table I.

3.1.3 Mating (monogamous, polygamous, promiscuous)

Since the mating of groupers has never been observed there is no information on this phase of life history.

3.1.4 Fertilization (internal, external)

The absence of intromittent organs seems to indicate that fertilization is external.

3.1.5 Fecundity

- Relation of gonad size and egg number to body size and to age

Table II lists a few egg counts which have been made in certain species of groupers. While it is evident that groupers produce large numbers of eggs this gives us little information as to fecundity since it has not been established how long the individual fish remain in the functional female stage.

Table I

SUMMARY OF HISTOLOGICAL STUDIES ON GONADS OF SERRANIDAE
(Numbers in parentheses indicate range of standard length in millimeters)

Species	Females	Males [1]	Total
Epinephelus striatus	41 (142-417)		41
E. guttatus	80 (114-385)	26 (217-350)	106
E. itajara		1 (1602)	1
Cephalopholis fulva	23 (112-240)	18 (201-320)	41
Petrometopon cruentatum	19 (117-246)	3 (203-259)	22
Alphestes afer	7 (132-235)	1 (213)	8
Mycteroperca venenosa	4 (249-489)		4
M. bonaci	14 (286-515)	7 (1000-1150)	21
M. tigris	23 (155-214)	5 (387-618)	28
M. interstitialis	9 (223-321)		9
Paranthias furcifer [2]	3 (224-273)	1 (197)	4
Rypticus saponaceus [2]	5 (130-263)	1 (263)	6
Prionodes phoebe	synchronous hermaphrodites		2
Hypoplectrus unicolor	synchronous hermaphrodites		2

[1] All specimens in which development of male tissue could be detected are listed as males. The slow regression of some oocytes makes it impractical to distinguish between males and transition stages.

[2] Data inconclusive; perhaps these two species are gonochoritic.

Table II

EGG COUNTS FOR SOME GROUPERS

Species	Standard Length (mm)	Weight of Gonad (g)	Weight of Sample (g)	Number of Eggs in Sample	Calculated Number of Eggs in Gonad
Epinephelus guttatus	358	25.3	0.4	353	233,237
Epinephelus striatus	445	90.7	0.032	277	785,101
Mycteroperca venenosa	-	120.8	0.85	1003	1,425,443
Mycteroperca bonaci	805	587.2	0.8	686	5,035,240

3.1.6 Spawning

- Spawning seasons (beginning, end, peak)

As may be expected there is a wide variation in time of spawning depending on the latitude (temperature ?). Erdman (1956 and personal communication) records the following times of spawning (indicated by the presence of ripe fish) in the Puerto Rican waters: Cephalopholis fulva - December; Epinephelus guttatus - January; Mycteroperca bonaci - February; M. venenosa - April. In May of 1958 the author observed Mycteroperca bonaci in spawning condition on the Campeche Bank but during July and August of 1957 none of the several species examined at Bimini B.W.I. were in spawning condition. In Bermuda the spawning season for most species seems to extend from the middle or latter part of April to near the end of August with the peak of activity in June and July. Randall and Brock (1960:11) observed that certain Indo-Pacific species spawned intermittently, the peak of spawning activity coming a few days before the time of the full moon. Perhaps the same is true of some or all of the Atlantic species. There are no data on the time of day at which the spawning takes place.

3.1.7 Spawning grounds

- Coastal (surface, vegetation, shore, shoal, sand shelter); bottom

In the absence of evidence of spawning migrations it appears that most species spawn in their usual habitat, i.e. in depths of from two to 100 fathoms. Bermuda fishermen report that during the early part of the spawning season some of the Nassau groupers taken on the offshore banks are distinctly more reddish in color than those taken at other times. This may indicate a migration from the deeper slopes of the banks. The actual manner of the deposition of the eggs remains unknown as does the spawning behaviour.

3.1.8 Egg: structure, size, hatching type, parasites and predators

The eggs are slightly under 1 mm in diameter (as determined from dissections of ripe ovaries) with a large peripheral oil droplet. There are no holdfasts or other modifications and it is assumed that the eggs float freely near the surface of the open sea.

3.2 Larval history

3.2.1 Account of embryonic and juvenile life (prelarva, larva, postlarva, juvenile)

Here again there is an almost complete lack of information. It is assumed that the egg is pelagic and that the early larval stages are also, but the larvae have not yet been described. Bardach, Smith and Menzel (1958) reported that late larvae taken at the surface of the open sea near Bermuda were kept in an aquarium until they transformed. These newly transformed groupers were kept a few days, then preserved and later identified as Epinephelus striatus and Alphestes afer. The standard lenths of these two specimens were 45.6 mm and 37.5 mm respectively. The size at transformation seems to be dependent on many factors, for individuals much smaller than these have been collected in the Bahamas indicating that transformation may be delayed until the proper environment is encountered.

Newly transformed groupers generally resemble the adults except that they have elongate serrated spines at the angle of the preopercle and in the dorsal, anal, and pelvic fins. Such spines appear to be remnants of elongate spines in the pelagic larvae suggesting that the larvae of groupers are similar to those which have been described for other serranid fishes, e.g. the larvae of Serranus hepatus as illustrated by Fage (1918). Such larvae have been found in Bermuda waters during the grouper spawning season but in the absence of intermediate stages we cannot be certain of their identity.

There is no distinctive juvenile body form but the color pattern of the juveniles of Mycteroperca interstitialis is grossly different from that of the adult. In that species the juvenile is sharply bicolored, very dark above and white below. Because of this conspicuous coloration we have an indication of the length of the larval period in that species in Bermuda waters. In the summer of 1956 members of the Bermuda fisheries research program were actively engaged in making underwater observations. In the course of other work the sudden appearance of these distinctive juveniles was noted about the first of August, although it was several days later before we were able to secure specimens for positive identification. Assuming the spawning season to have begun near 1 April (and probably not this early), four months had been sufficient for the egg, pelagic, and early juvenile stages. There is no more direct information as to the duration of the larval stages.

3.3 Adult history

3.3.1 Longevity

Because no adequate growth and age studies have been reported we have no data on the length of life of groupers in the wild state, but Townsend (1905) reported that adult Nassau groupers (Epinephelus striatus) survived for more than seven years in the old New York Aquarium.

3.3.2 Hardiness

In general groupers are rather hardy fishes, easily kept in aquaria and in live wells of fishing vessels. They may be susceptible to low temperatures but the author knows of no published studies on this point. When brought to the surface from considerable depths the expansion of the swim bladder often everts the stomach but operations to puncture the air bladder and replace the organs are frequently successful.

3.3.3 Competitors

In the complex economy of the shallow water environment it is difficult to evaluate the effects of competition between species. Inasmuch as groupers are unspecialized carnivores it appears that we may well assume that they compete for food with all large and small carnivores of the same area. Probably the species occupying the econiches closest to any given species of grouper is another grouper. Since groupers have stringent requirements as to shelter and space the number of suitable hiding places in an area may at times be a limiting factor.

3.3.4 Predators

So few food studies have been made on reef fishes that there are really no data available on the predation of groupers. Large individuals readily feed on smaller members of the same or other species but it is doubtful if other fishes can prey upon the larger groupers effectively.

3.3.5 Parasites and diseases

Manter (1947) has listed the following species of trematodes from groupers taken in the vicinity of the Tortugas Islands, Florida:

Table III

SPECIES OF TREMATODES FROM GROUPERS TAKEN IN THE VICINITY OF THE TORTUGAS ISLANDS, FLORIDA

Host	Number Examined	Trematodes
Epinephelus adscensionis	1	Stephenostomum dentatum (Linton)
E. morio	33	Helicometra torta Linton
		Lepidapedon levenseni (Linton)
		Opisthoporus epinephely Manter
		Stephanostomum dentatum (Linton)
E. niveatus	3	Lepidapedon nicolli Manter
		Prosorhynchus ozakii Manter
		Stephanostomum microstephanum Manter
E. striatus	6	Helicometra torta Linton
		Lecithochirum parvum Manter
Mycteroperca microlepis	1	Prosorhynchus atlanticus Manter
M. venenosa	7	Helicometra execta Linton
		Opisthoporus mycteropercae Manter
		Prosorhynchus atlanticus Manter
		Stephanostomum dentatum (Linton)
Promicrops itaiara	4	Lecithochirium microstomum Chandler
(Epinephelus itajara)		Prosorhynchus promicropsi Manter
		Stephanostomum promicropsi Manter

In addition to these trematodes, some grouper species have almost 100 per cent infection with larval tapeworms which appear as cysts in the visceral cavity. Occasionally nematodes are found in the gonads and cases of the invasion of the body cavity by sharp-tailed eels have been reported (Breder and Nigrelli, 1934)

3.4 Nutrition and growth

3.4.1 Feeding (time, place, manner, season)

Bardach and Menzel (1957) have studied nutrition and growth in Epinephelus guttatus, Epinephelus striatus, and some species of Mycteroperca. Their results and observations by the author indicate that most species feed throughout the day whenever food is available, for most species will take a hook at any hour. Bardach and Mowbray (1955) suggested that the final steps in feeding are visual, thus, there is apt to be a decrease in feeding activity during the hours of darkness. Randall and Brock (1960) noted that the highest proportion of full stomachs were found during the morning hours. Possibly this is an indication that the peak of feeding comes around sunrise.

Most groupers feed close to the bottom although Mycteroperca tigris will rise from depths of 50 feet or more to take a lure trolled near the surface.

3.4.2 Food (type, volume)

Observations incidental to other studies indicate that fish and crustacea are the chief items in the diet of most groupers. (Bardach and Mowbray, 1955; Randall and Brock, 1960). Larger fishes seem to eat more fishes and smaller individuals take more crustacea although the largest species in the Western Atlantic, Epinephelus itajara, feeds chiefly on crustacea (personal observations and Erdman, 1956). This is probably a specialization among groupers and is reflected in the reduction of the canine jaw teeth.

3.4.3 Relative and absolute growth patterns and rates

Bardach and Menzel (1957) found growth rates for tagged and recaptured red hinds, Epinephelus guttatus, to be around 20 to 25 per cent of the body weight annually during the winter months and about 40 per cent per year during the summer months. As was expected, larger fish grew more slowly than small individuals of the same species. Experiments in which small red hinds were held in captivity and fed to satiation indicated that for short periods growth rates of over 200 per cent per year could be achieved under proper temperature conditions.

3.5 Behaviour

3.5.1 Migration and local movements

Bardach (1958a) in a series of tagging experiments conducted on the Bermuda reefs found that red hinds, Epinephelus guttatus, and Nassau groupers, Epinephelus striatus, tended to remain on a given isolated reef for periods of a month or more but there was a gradual exchange of individuals and after a year the original population had been replaced. Within the confines of one isolated reef it appeared that the Nassau groupers moved somewhat more than the red hinds. In one series of experiments blinded fishes were unable to return to their home reef but one out of seven red hinds with plugged nares was able to return to its home reef from another reef some 500 meters distant. Croizer (1918) and Jordan (1917) demonstrated that Nassau groupers have well developed tactile responses which presumably aid the fish in locating themselves in the reef environment.

3.5.2 Schooling

Groupers are essentially solitary animals and although a favorable environment will harbor many individuals there is no sign of interaction between them. Paranthias furcifer is reported to school but this is probably a loose aggregation such as is seen in the various species of grunts (Haemulon sp.).

3.5.3 Reproductive habits

There has been no report of the reproductive behaviour of any species of grouper.

4 POPULATION (STOCK)

4.1 Structure

4.1.1 Sex ratio

Most of the groupers here considered are proterogynously hermaphroditic, therefore the sex ratios are directly related to the size and age of the individuals in the population. At the present time we have only an indication of the sizes at which the sex reversal takes place but further studies can determine statistically the sex ratios for each given size range. This information will be of great importance for management of the fishery because any control of the sizes of the individuals in the harvest will also be a control of the sex ratio of the individuals taken. By appropriate size limits the catch can be restricted to one sex or the other or to any proportions of the sexes.

4.1.2 Age composition

At present there are no data on age since the scale marks have not yet been interpreted. Marks do appear on the scales of most species but it has not been established that they correspond to annual interrruptions of growth.

4.1.3 Size composition

One of the most striking characteristics of grouper populations is the comparative rarity of small individuals. Bardach (1958a) noted that the groupers under four inches in length are exceedingly rare in Bermuda waters. Bardach, Smith and Menzel (1958) presented length-weight curves for several species of Bermuda groupers and from these data we can approximate the size composition of the Bermuda populations. Maximum, minimum and average lengths are given as follows:

Table IV

SIZE COMPOSITION OF SOME GROUPERS FROM BERMUDA
(All lengths are standard lengths in mm)

Species	Number of Measurements	Smallest	Larger	Average
Epinephelus guttatus	114	140	420	302.6
E. striatus	141	175	755	510.1
Cephalopholis fulva	108	147	335	219.6
Petrometopon cruentatum	4	148	230	188.8
Mycteroperca bonaci	17	297	940	615.8
M. tigris	89	238	810	483.1
M. venenosa	9	320	790	476.8
M. interstitialis	28	155	543	416.4

A distinct difference in size between fishes taken on the offshore banks of Bermuda (Challenger and Argus) and those taken near the islands was ascribed to the relative fishing pressure in the two areas. The difference was also taken as an indication that the adult populations of the banks are distinct from that of the inshore areas (Bardach, Smith and Menzel, 1958). Nassau groupers from the inshore reefs have a size mode at 250 mm; those from the banks had a mode between 500 and 600 mm standard length.

4.2 Size and density

Perhaps the greatest need in studies of coral reef fishes today is for adequate census methods. All of the gear used for commercial harvesting of groupers is highly selective and other methods such as poisoning an enclosed area and direct observation have serious drawbacks. The most complete data now available are those of Bardach (1959) which were obtained by marking and recapture methods and checked by repeated counts made by divers using self-contained underwater breathing apparatus. These data are summerized as follows:

Species	Average Weight in Grams	Number per Hectare	Kilograms per Hectare
Epinephelus guttatus	600	43	25.8
E. striatus	1115	10	11.2
Mycteroperca spp.	1500	11.3	17.0
Cephalopholis fulva	400	7	2.8

These figures are averages of observations made over a three year period. Some changes may be expected according to the season and other environmental factors but data pertaining to such changes are not available.

4.6 Relation of population to community and ecosystem, biological production, etc.

From the foregoing statements it is clear that very little quantitative information on grouper populations is available. It is to be hoped that this situation will change in the near future for with the development of more intensive fisheries in tropical areas groupers will certainly come to be important commercial fishes. In addition to the practical need for such information, there is a more basic reason for studying the population dynamics of these species. Groupers as unspecialized carnivores stand at the end of many food chains in the reef environment, thus occupying a position of prime importance in the overall economy of the reef areas.

5 EXPLOITATION

5.1 Fishing equipment

5.1.1 Fishing gear

Because of the nature of the habitat, groupers are taken chiefly on hand lines and in fish pots (arrowhead traps). Occasionally small juveniles are taken in beach seines and during recent exploratory fishing operations on the Campeche Banks by the United States Fish and Wildlife Service groupers were taken in some quantity by means of otter trawls fitted with roller gear (Rathjen, 1959).

5.1.2 Fishing boats

Most of the vessels used in the grouper fisheries of the western Atlantic are under 20 tons and in many areas sail driven vessels are still in use. The degree of mechanization varies but power winches and power-driven reels are used in only a few places (Caabro, 1957; Carranza, 1957).

5.2 Fishing areas

5.2.1 General geographic distribution

Groupers make up parts of the commercial catch throughout the West Indies and Bermuda. In 1957 significant landings were reported from United States ports along the northern Gulf coast, Florida, and as far north as North Carolina on the Atlantic coast. Perhaps some of these catches were made on the Campeche Bank. Martin (1959) indicates that there is a considerable fishery in Venezuela. Figures do not seem to be available for the South American coast south of Trinidad but it may be assumed that the fishery is not highly developed in that region. Although the quantities landed are not large there are many areas in which there is a high preference for groupers and this is an important factor in the salability of the catch.

5.2.2 Geographical ranges (latitudes, distances from coast, etc.)

Most of the fishing for groupers is carried on within a few miles of the home port although even small sailing vessels sometimes make trips of up to 25 miles from their home base. The Campeche Bank fishery is an exception and here Cuban and American vessels make trips lasting 20 days or longer.

5.2.3 Depth ranges

Under existing conditions where little mechanization is employed, most of the fishing is done in depths of 30 fathoms or less. Bardach (1958b) has suggested that mechanical aids might extend the fishing depths to the 100 fathoms line which would greatly increase the area that could be fished.

5.3 Fishing seasons

5.3.1 General pattern of fishing season

Groupers are essentially tropical and subtropical fishes and the season is potentially all year long. Caabro (1957) gives catch data for certain Cuban vessels during 1955 which indicate lowered landings during the winter and early spring months (January, April through June). These, however, may have been due to unusual conditions and not indicative of any real seasonal fluctuations. In Bermuda, where weather conditions are more severe, Bardach and Mowbray (1955) reported that the catch is decreased by 60 per cent during December and March and by 80 per cent during January and February.

5.3.5 Factors affecting fishing season

In general it may be stated that the weather is the chief factor in limiting the fishing season. Caabro (1957) mentions that during the summer and especially during the hurricane season, Cuban vessels may shift their operations from Campeche Bank to the west coast of Florida. In Bermuda the danger of storm loss of fish pots limits the winter fishery and there is some suggestion that fish are less readily available during the colder months. Whether this is due to a local migration to deeper water or the result of lessened activity of the fish at lower temperatures has not been determined. The spiny lobster season in Bermuda extends from September to April and during that period much of the fishing effort is directed toward the lobsters which provide higher cash returns. Occasionally the market demand for fish drops off at certain seasons (summer in Bermuda) and this influences the intensity of the fishing effort.

5.4 Fishing operations and results

5.4.1 Effort and intensity

Because of the low technological development of the fishery in most areas it may be safely assumed that the grouper fishery operates at a low level of intensity. Bardach and Menzel (1957) estimated a harvest of 10 to 15 per cent of the yearly weight increase on commercially usable fishes (mostly groupers) on the Bermuda reefs. They suggest that this harvest could be increased 50 to 70 per cent using present methods. Although no figures are available for other western Atlantic areas it would appear that substantially greater harvests could be realized with increased fishing effort and intensity.

5.4.2 Selectivity

The handline fishery is quite selective for groupers and snappers (Lutjanus spp.) and only insignificant numbers of other species are taken in this way. Arrowhead traps are also selective although other carnivores and some omnivorous species are taken as well. In Bermuda the market is highly selective

for groupers and most of the other species taken are used for bait or are released. Caabro (1957) indicated that over 90 per cent of the fish taken on the Campeche Bank by the Cuban grouper and snapper boats are groupers.

5.4.3 Catches

In 1957 the total grouper landings in the United States amounted to 7,630,000 lbs having a value of $767,000.00 (Power, 1959). Bardach and Menzel (1957) reported landings in Bermuda of slightly under 1,000,000 lbs. Complete figures are not available for other regions but some indication of fishing success may be gleaned from the following statements. The larger Cuban vessels which fish the Campeche Bank and west Florida coast areas carry crews of 10 or 11 handline fishermen. These vessels land between 8,000 and 15,000 lbs per trip of 16 to 19 days' effective fishing, or approximately 50 to 100 lbs per man per day. In Bermuda the average catch per trap per hour is 3.45 lbs when the traps are set in water 2 to 9 fathoms deep and 7.13 lbs when the traps are set in water 10 to 30 fathoms deep. An average day's catch in Bermuda for a fishing boat with two men is 90 lbs. Most vessels fish 135 days per year (Bardach and Mowbray, 1955).

5.5 Fisheries management and regulations

At present there is virtually no regulation of the grouper fishery. In Bermuda there are some regulations pertaining to the minimum size of fish landed but these are not strictly enforced. The market itself imposes some restrictions for fish that are too small and not readily marketed. Unfortunately this has the general effect of eliminating some of the smaller species (*Epinephelus guttatus*, *Petrometopon cruentatum*, and *Cephalopholis fulva*) from the catch. The author knows of no other regulations at the present time and in view of the low level of technical development and the paucity of knowledge about the grouper fishery it would seem that regulation would be premature.

5.6 Fish farming, transplanting and other intervention

No efforts at artificial propagation of groupers have been reported and the author is not aware that any transplantation efforts have been successful.

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